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Primary productivity and decomposition in fens and marshes in the boreal region of Alberta, Canada

by

Markus Norbert Thormann ©

A thesis submitted to the Faculty of Graduate Studies and Research
in partial fulfillment of the requirements for the degree
of Master of Science

in

Plant Ecology

Department of Botany

Edmonton, Alberta

Fall, 1995

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The undersigned certify that they have read, and recommended to the Faculty of Graduate Studies and Research for acceptance, a thesis entitled *Primary production and decomposition in fens and marshes in the boreal region of Alberta, Canada* submitted by *Markus Norbert Thormann* in partial fulfillment of the requirements for the degree of *Master of Science* in *Plant Ecology*.

Suzanne Bayley

Prof. Suzanne E. Bayley

M. Hickman

Prof. Michael Hickman

Jens Roland

Prof. Jens Roland

September 27, 1995

Für meinen Papa Wolfgang und Opa Heinz und Oma Paula, ich wünschte ihr wärt hier und könntet dies mit mir erleben, und meinen Eltern und Verwandten in Kanada und Deutschland. Vielen Dank für Eure Hilfe und Eurem Glauben an mich über die vergangenen Jahre.

Abstract

Net primary production (NPP), decomposition, changes in C, N and TP tissue concentrations and responses to N or P fertilization of aboveground vascular vegetation along a bog - fen - marsh peatland gradient in central Alberta, Canada, were measured during the 1993 and 1994 growing seasons. The peatlands were a bog, an open rich fen (ORF), a lacustrine sedge fen (LSF), a riverine sedge fen (RSF), a riverine marsh (RM) and a lacustrine marsh (LM).

Total plant NPP of the bog and the fens were similar but significantly lower than that of the marshes. The plant production values obtained conform to a latitudinal gradient for North American wetlands, although the marshes of this study were substantially less productive than Canadian counterparts at similar latitudes. Moss and herb production varied significantly between years and among sites, whereas shrubs production only varied significantly among sites but not years.

Litter quality and the surface water nutrient status of the sites partially explained the rates of decomposition of the dominant and standard plant litters and cellulose (filterpaper) over varying lengths of time. Decay of the plant litter was similar in fens and marshes, but cellulose decomposed significantly faster in the eutrophic marshes than in the oligotrophic fens. Nitrogen and phosphorus surface water parameters related best to litter decay in these peatlands. The carbon to nitrogen (C:N) ratio changes during plant litter decay depended on the litter type and quality and the surface water nutrient concentrations within sites. The nutrient status of the site, plant species, life history and stand density partly explained the C:N ratio changes throughout the growing season. Generally, C:N ratios decreased towards late August.

Fertilization with N or P generally did not reveal which nutrient limits plant production in Alberta peatlands. In the bog, ericaceous and deciduous shrubs, mosses and herbs were variable in their responses to fertilization. Fen and marsh plant species generally did not respond significantly to N or P addition, possibly due to luxury consumption of the fertilizers or immediate microbial uptake.

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List of Abbreviations and Symbols

Sites

B - Bog
LM - Lacustrine marsh
LSF - Lacustrine sedge fen
ORF - Open rich fen
RM - Riverine marsh
RSF - Riverine sedge fen

Ecological Measurement Terms

Decomp. - Decomposition
GDD - Growing degree days
ha - Hectare (10,000 m^2)
k - % weight remaining
k' - % weight loss
k_{SE} - Simple exponential decay constant
NPP - Net primary production
Precip. - Precipitation
Prod. - Production
t - Time
Temp. - Temperature
X - Final weight
X_0 - Initial weight

Chemical Terms

Alk. - Alkalinity
C - Carbon
Ca^{2+} - Calcium ion
CH_4 - Methane
CO_2 - Carbon dioxide

^{o}C - Degrees Celcius
C:N - Carbon to nitrogen ratio
Conduct. - Conductivity
g - Gram
HCO_3^- - Bicarbonate ion
K^+ - Potassium ion
L - Litre
Mg^{2+} - Magnesium ion
mL - Millilitre
N - Nitrogen
Na^+ - Sodium ion
NH_4NO_3 - Ammonium nitrate
NH_4^+ - Ammonium ion
NO_3^- - Nitrate ion
NO_2^- - Nitrite ion
N_2O - Nitrous oxide
P - Phosphorus
SO_4^{2-} - Sulfate ion
SRP - Soluble reactive phosphorus
TDP - Total dissolved phosphorus
TP - Total phosphorus
2d-H_20 - Double distilled water

Statistical Terms

ANCOVA - Analysis of co-variance
ANOVA - Analysis of variance
corr. - Correlation
Dunn. - Dunnett's test
ln transf. - Natural logarithm transformed
n - Sample size
n.d. - Not determined
n.s. - Not significant ($p > 0.05$)
p - Probability
r - Correlation coefficient

sqrt. transf. - Square-root transformed
x - Independent variable
y - Dependent variable
> - Greater than
< - Less than

1. INTRODUCTION

Peatlands cover approximately 14% (127.2 million ha) of Canada's boreal region and they are defined as wetlands where the organic matter has accumulated to a depth of at least 40 cm (Natural Wetlands Working Group, 1988).

Bogs, fens and marshes differ in their hydrology, water chemistry, species diversity and composition, productivity and decomposition and peat accumulation. Bogs are ombrotrophic systems which receive nutrients from precipitation and are isolated from mineral-rich groundwater. Their surface water is strongly acidic and the upper peat layers are deficient in nutrients and oxygen saturation is minimal. Fens and marshes are minerotrophic ecosystems which receive nutrients from groundwater, precipitation and run-off. Their surface water ranges from being slightly acidic to being neutral and alkaline, and the nutrient content of the surface water and peat is usually higher than in bogs. While oxygen saturation is still fairly low in fens, it is usually high in marshes. Fens can be further subdivided into poor fens and rich fens on the basis of moss indicator species (*sensu* Du Rietz, 1949) and pH/alkalinity (Sjörs, 1950). Poor fens, like bogs, are dominated by *Sphagnum* spp. and have a low number of indicator species, such as *Drepanocladus exannulatus*, *Sphagnum angustifolium*, *Sphagnum jensenii* and *Sphagnum majus* (Vitt & Chee, 1990). Rich fens are dominated by brown mosses and have a relatively high number of indicator species, such as *Brachythecium mildeanum*, *Drepanocladus vernicosus*, *Drepanocladus aduncus* and *Drepanocladus polycarpus* (Vitt & Chee, 1990). Marshes are characterized by the absence of moss indicator species and are dominated by sedges, rushes and reeds. A wet mineral soil predominates in many areas but shallow, well decomposed peat may be present as well (Natural Wetlands Working Group, 1988). The marshes described in this thesis have a peat substrate.

Peat accumulation may be more related to slow rates of decomposition rather than high rates of production (Clymo, 1965; Malmer, 1986; Farrish & Grigal, 1988; Vitt, 1990). Simultaneous studies of decomposition and productivity rates in bogs, fens and marshes are limited (Reader & Stewart, 1972; Bartsch & Moore, 1985). Few studies document the relationship of these two processes with hydrological and other environmental factors (Forrest & Smith, 1975; Farrish & Grigal, 1988; Moore, 1989). It is widely accepted that bogs have a greater peat accumulation rate than both fens (Malmer, 1986) and marshes (Natural Wetlands Working Group, 1988). Furthermore, rates of organic matter accumulation can vary between similar sites and between sites within the same geographical region (Gorham, 1982).

Production (net primary production; NPP), is the growth of all non-vascular and vascular plants and it is expressed as $g/m^2/day$ or as $g/m^2/year$ (Mitsch & Gosselink, 1993). Production is influenced by plant physiology and morphology, such as vertical orientation of the leaves and hybrid vigor, as well as chemical, such as nutrient availability, and environmental factors, such as temperature, moisture availability, length of the growing season and amount of solar radiation (Brinson et al., 1981; Chapin III et al., 1988).

Decomposition, synonymous with decay, is the sum of all changes of organic matter after death or senescence of the plant. These changes arise from passive physical processes or from the activity of decomposers on the plant matter (Brinson et al., 1981). The highest rates of decomposition occur under aerobic conditions and an optimal regime of wetting and drying and result in the liberation of nutrients, thus, making them available to growing plants. In forest humus, the C:N ration of the decaying plant matter changes during the process of decomposition and the rate of decay may be influenced by the quality of the litter (McClaugherty et al., 1985).

The objectives of this thesis were to determine the rates of aboveground plant production and the rates of decomposition in six peatlands in central Alberta, Canada, ranging from one bog to three moderate-rich to rich fens to two eutrophic marshes and to relate NPP and decay to hydrology, water chemistry and climatic factors. Hydrology is an important factor in peatland succession due to its control over the aeration/redox potential of substrates and the transport and availability of all nutrients which influence both production and decomposition. Nutrients such as N and P in the surface water received special attention due to their importance in determining plant growth (Reader, 1978) and their influence on the activities of decomposers. Furthermore, decomposition is strongly influenced by the pH and associated characteristics, such as alkalinity, conductivity and Ca^{2+}. Climatic variables, such as precipitation, growing degree days (GDD) and temperature, were examined to explain some differences between years and results of other studies.

Chapter two focuses on the aboveground NPP of six peatlands (five in 1993 and an additional sixth in 1994) and it includes mosses, herbs, shrubs and trees. Herbs include both graminoids and forbs, while the shrub layer includes deciduous and evergreen species. The NPP of the tree stratum results from seedlings and large individuals of coniferous species. I hypothesize that an increasing gradient in the primary plant production from the bog to fens to eutrophic marshes exists in central Alberta, Canada, due to the increasing elevation of the surface water, higher pH and increasing nutrient inflow. This study differs from that of Szumigalski & Bayley (under review), which examined a plant production gradient from bogs to poor, moderate and extreme-rich fens in the same area in 1991 and 1992, but it did not include marshes.

Chapter three examines the rates of decomposition, which were measured as percent weight loss of the decomposing litter over time. Three decomposition studies were carried out in all sites except the bog during 1993 and 1994. Dominant native litter decomposed over a 456 day period starting in 1993. Cellulose (filterpaper) and a standard plant substrate decomposed over a 100 day period in 1994. I hypothesize that there is an increasing gradient of decomposition from fens to eutrophic marshes for all three litter types due to higher water levels and the associated higher surface water nutrients in the eutrophic marshes. I also hypothesize that the differences in decomposition rates are based on litter quality (N content and C:N ratio) and that the C:N ratio will decrease for the two plant litter types over time in all sites.

Chapter four examines the relationship of environmental parameters (water levels and surface water chemistry) to NPP. I hypothesize that higher water level results in higher plant production within each study site due to the greater availability of water and the associated nutrients. Sedges are perennials with a life-span up to seven years (Bernard & Gorham, 1978). In most cases, shoots die after one growing season but they too can survive for up to two years (*Carex rostrata*) (Bernard & Somers, 1978). Generally, perennial plant species translocate nutrients from shoots to roots before senescence in order to build reserves in their belowground tissues. These nutrients are then used to initiate shoot growth in the following growing season (Gorham & Somers, 1973). Thus, I hypothesize that %C, %N and total phosphorus concentrations in shoots will decrease towards the end of the growing season.

Chapter five examines the effects of N or P fertilization on vascular and non-vascular plant production within all sites except the open rich fen. The effects on total plant production as well as specific species are investigated. Most terrestrial and aquatic boreal ecosystems are either nitrogen and/or phosphorus limited. Organic soils generally have large amounts of nutrients tied up in organic forms but these are not available to plants. In fact, many of the nutrients in peatland soils, such as phosphorus, are unavailable and may limit plant productivity (Mitsch & Gosselink, 1993). I hypothesize that by fertilizing the vegetation with N or P, I will be able to determine which of the two major nutrients is limiting within each peatland by comparing the productivity of fertilized to unfertilized plots within the tested sites. I also hypothesize that herbs and deciduous shrubs will show a greater response to N and P fertilization than ericaceous shrubs due to their life histories.

Chapter six focuses on the effect of the water level on decomposition and production rates within the lacustrine sedge fen and the bog over a four year period from 1991 to 1994. Peatlands play an important role in the exchange of elements with the atmosphere and may contribute to the accumulation of greenhouse gases in the atmosphere. Conversely, peatlands and muskegs in northern Canada represent large carbon sinks (Gorham, 1991).

Numerous global climate models (GCMs) predict that the atmospheric temperature will increase (Robock, 1993; Wigley & Jones, 1990; Schneider, 1989), and Gorham (1991) predicted that these temperature increases will lead to higher water tables and thermokarst in northern ecosystems. This may result in increased CO_2 and CH_4 (both greenhouse gases) emissions from peatlands due to the oxidation of peat (Gorham, 1991). Also, a resurgence of peat formation may result in peatlands which have not accumulated much peat in the past (Gorham, 1991). I hypothesize that a lowering of the water table will result in lower herb and moss production. I also hypothesize that shrub production will increase and that surface water nutrient concentrations will decrease if water levels drop in response to warmer climates. Lastly, I hypothesize that tissue nutrient concentrations of N and TP will decrease in response to a lowered water table due to decreased nutrient concentrations in the surface water. If the atmospheric temperature does not increase in the future, any significant changes in decomposition and production between 1991 and 1994 must be attributed to short term microenvironmental fluctuations in these two peatlands.

Chapter seven is a summary and integration of the major results of Chapters two, three, four, five and six with a brief concluding discussion.

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2. ABOVEGROUND NET PRIMARY PRODUCTION ALONG A BOG - FEN - MARSH GRADIENT IN BOREAL ALBERTA.

Introduction

Peatlands cover approximately 14% of Canada's and 21% of Alberta's surface (Natural Wetlands Working Group, 1988). They are defined as waterlogged ecosystems (Gorham, 1991), where plant production exceeds the rate of decomposition (Zoltai, 1988) and the peat thickness is greater than 30-40 cm (Gorham, 1991). Peatlands are among the world's most important ecosystems (Natural Wetlands Working Group, 1988) and just recently have become sources, sinks and transformers of a multitude of chemical, biological and genetic materials (Mitsch & Gosselink, 1993). Therefore, peatlands have great economic, recreational, agricultural, water resource, wildlife and fishing values (Alberta Water Resources Commission, 1993).

Several European and North American studies have examined non-vascular and vascular aboveground net primary production (NPP) (Mason & Bryant, 1975; Forrest & Smith, 1975; Vasander, 1982; Francez, 1992; Reader & Stewart, 1972; Bartsch & Moore, 1985; Griegal et al., 1985; Wieder et al., 1989). The vast majority of these studies were conducted in tundra/sub-arctic or deciduous forest regions. Despite Alberta's wealth of peatlands, most studies have concentrated on either bryophyte (Busby et al., 1978; Vitt, 1990) or sedge (Gorham & Somers, 1973) NPP and only recently has a study been carried out which examined the total net primary production along a bog - extreme-rich fen gradient in this region (Szumigalski & Bayley, under review).

I examined five peatlands in 1993 and 1994 and an additional sixth in 1994 in central Alberta, Canada. They were: a bog, three moderate-rich to rich fens and two eutrophic marshes. These peatlands represent a gradient based on the elevation of surface water, inflow of nutrients, vegetation type, pH and peat accumulation characteristics (Mitsch & Gosselink, 1993). Bogs are ombrotrophic, acidic, *Sphagnum* spp. dominated peatlands which receive nutrients only from precipitation. Fens and marshes are minerotrophic peatlands which receive nutrients from precipitation as well as from surface and groundwater flow. Their pH is less acidic to neutral. Fens are dominated by "brown" mosses, sedges, grasses and shrubs and they are mesotrophic with organic soil. Marshes are generally eutrophic peatlands which are dominated by sedges, reeds and grasses with shrubs and mosses generally lacking. Sjörs (1950) determined that the pH, relative conductivity and Ca^{2+} and the number of indicator species increases from bogs to fens. However, this may not be the case for nitrogen (N) and phosphorus (P) in the surface water (Malmer, 1986). However, fens may still receive more nutrients than bogs due to their greater in- and efflux of water (Sparling, 1966). Marshes are usually eutrophic and have the highest concentrations of N and P (Mitsch & Gosselink, 1993), and Sjörs' (1950) increasing gradient of pH, relative conductivity and Ca^{2+} can be extended from fens to marshes (Mitsch & Gosselink, 1993). In addition, peat depth is generally greater in bogs than in fens (National Wetlands Working Group, 1988). Marshes are characterized by the presence of a wet mineral soil in many areas but a shallow, well decomposed layer of peat may be present in some areas as well (National Wetlands Working Group, 1988).

In this chapter, I will present the vascular and total aboveground net primary plant production values for a bog, three moderate-rich to rich fens and two eutrophic marshes in central Alberta. I hypothesize that the NPP increases from bogs to fens to marshes.

Study area and site descriptions

The five study sites which were examined in 1993 and 1994 and an additional sixth in 1994 represent the range of peatlands present in the southern boreal region of western Canada. These included a bog, an open rich fen (ORF), a riverine sedge fen (RSF), a lacustrine sedge fen (LSF), a riverine marsh (RM) and a lacustrine marsh (LM). The bog is located north of Bleak Lake at 54° 41' N and 113° 28' W, while the ORF (54° 28' N, 113° 17' W), LSF (54° 28' N, 113° 19' W) and the RSF (54° 28' N, 113° 18' W) are located east of Perryvale. The RM is located northwest of Perryvale at 54° 28'N and 113° 23' W, and the LM is located northeast of Clyde (54° 10' N, 113° 34' W) (Figure 2.1.).

The climate of the area is characterized by mild summers and cold, snowy winters (Vitt et al., in press). The long term mean annual temperature is 1.7 °C (Environment Canada, 1982) and the total mean precipitation is approximately 500 mm for all sites. Appendix 1 summarizes the climatic data for the 1993 and 1994 growing periods for all sites and Vitt et al. (in press) give a detailed description of the vegetation and the water chemistry of the bog and the open rich fen. All six peatlands lie within the Boreal Forest Region of Canada (Rowe, 1972). The "brown" moss and *Sphagnum* nomenclatures follow Anderson et al. (1990) and Anderson (1990), respectively, while that of the vascular plants follows Packer (1983). Hepatics nomenclature follows Vitt et al. (1988).

Bog

The bog is a large, raised ombrotrophic island with 5 m of peat within a large peatland complex. The peat surface is raised about 0.3-0.5 m above an adjacent poor fen water track. The peat is arranged in large, dry hummocks, which are separated by intermittent wetter hollows. The pH of the open water in the hollows ranged from 3.7 to 4.1. A sparse tree layer of *Picea mariana* (Mill.) BSP. covers about 25% of the wooded part of the bog. *Ledum groenlandicum* Oeder dominates the ericaceous shrub layer (covers about 75%), while *Vaccinium vitis-idaea* L., *Oxycoccus microcarpus* Turcz. and *Andromeda polifolia* L. are also present. The sparse herb stratum consists of *Smilacina trifolia* (L.) Desf., *Rubus chamaemorus* L. and *Eriophorum vaginatum* L.. *Sphagnum fuscum* (Schimp.) Klinggr. comprises about 90% of the moss layer. *Sphagnum angustafolium* (C. Jens. *ex* Russ.) C. Jens. and *S. magellanicum* Brid. make up the remainder of this vegetation stratum on mid-hummocks while *Polytrichum strictum* Brid. can be found on dry hummocks. This site was studied by Szumigalski & Bayley (under review) in 1991 and 1992.

Lacustrine Sedge Fen

This site is a large expanse of sedge dominated peatland situated aside a large body of water (approximately 62 ha) in a former north-south drainage channel (Vitt et al., in press) with 2-2.5 m of peat. This fen's topography is mainly flat with the occasional small hummock (about 5% of the peatland surface). The lacustrine sedge fen was largely inundated with water for most of 1991, characteristic of a marsh, but began to dry out in 1992; therefore, Vitt et al. (in press) classified this peatland as an extreme-rich fen. In 1993, this site continued to dry out but in 1994 it was once again flooded, possibly due to beaver dams blocking outflows of the former drainage channel. The pH of the surface water ranged from 6.1 to 6.9. The vascular vegetation stratum consists primarily of *Carex lasiocarpa* Ehrh. and *C. diandra* Schrank. Other species present are *C. chordorrhiza* L.f., *C. limosa* L. and *C. aquatilis* Wahlenb.. Shrubs comprise only about 5% of the peatland cover and consist of *Salix pedicellaris* Pursh and *Betula pumila* L. *var. glandulifera* Regel exclusively. The moss stratum is discontinuous and dominated by *Drepanocladus aduncus* (Hedw.) Warnst., *Hamatocaulis vernicosus* (Mitt.) Hedenäs and *Calliergon giganteum* (Schimp.) Kindb. in wet pools and by *Aulacomnium palustre* (Hedw.) Schwaegr. on top of dry hummocks. This site was previously studied by Szumigalski & Bayley (under review) in 1991 and 1992, they referred to this fen as 'sedge fen'.

Riverine Sedge Fen

This peatland is part of an extensive wetland complex adjacent to the aforementioned lacustrine sedge fen and has an approximate peat depth of 1 m. The pH of the surface water ranged from 6.3 to 8.1 during 1993 and 1994. It receives water from a discrete inflow at the southern end, and an outflow at the northern end controls the water table height. The water table was above the peat surface during the 1993 and 1994 growing seasons. In the spring of 1994, a constructed dam blocked the outflow and as a result, the water table was substantially higher during the second growing season. The vascular vegetation strata are dominated by *Carex aquatilis*

Wahlenb., *C. rostrata* Stokes and *C. lasiocarpa* Ehrh., which together comprise about 95% of the cover. The remaining surface area is covered by *Equisetum fluviatile* L. and a few other herbs. Mosses are very sparsely distributed and *Drepanocladus aduncus* (Hedw.) Warnst., *Brachythecium mildeanum* (Schimp.) Schimp. *ex* Milde and *Tomenthypnum nitens* (Hedw.) Loeske are most dominant. The thalloid liverwort *Marchantia polymorpha* L. was also present.

Open Rich Fen

This fen is a floating mat surrounding a small body of water. The peat surface is a uniform carpet, which fluctuates with the water table of the associated slough. The peat is approximately 1 m thick floating over 1-1.5 m of water below which an additional 1-1.5 m of peat are located. The vascular plant strata are dominated by *Carex lasiocarpa* Ehrh.. Also, *Carex diandra* Schrank, *C. rostrata* Stokes and *C. limosa* L. are present and along with *Carex lasiocarpa* Ehrh. comprise about 90% of the vegetation cover. Other herbs present are *Triglochin maritima* L., *Potentilla palustris* (L.) Scop. and the insectivorous, perennial herb *Drosera rotundifolia* L.. The shrub layer consists predominantly of *Salix pedicellaris* Pursh, *Andromeda polifolia* L. and *Oxycoccus quadripetalus* Gilib.. The moss stratum is dominated by *Calliergonella cuspidata* (Hedw.) Loeske, *Hamatocaulis vernicosus* (Mitt.) Hedenäs, *Sphagnum warnstorfii* Russ. and *Aulacomnium palustre* (Hedw.) Schwaegr.. The latter two species comprise about 80% of the moss cover in this fen. The pH of the surface water ranged from 5.5 to 7.4 during the 1993 and 1994 growing seasons.

Riverine Marsh

This site is located on the floodplain of Tawatinaw River. During 1993, this marsh was periodically inundated with water and the water table was consistently above the peat surface. In 1994, a beaver dam just above the study area retained much of the stream flow and the water table dropped well below the peat surface. The pH of the surface water ranged from 7.1 to 8.4 and the peat is less than 1 m deep. The vascular vegetation layer is dominated by *Carex* *aquatilis* Wahlenb., *C. rostrata* Stokes and *C. atherodes* Spreng. during spring and early summer with *Calamagrostis canadensis* (Michx.) Beauv. and *C. inexpansa* A. Gray dominant during late summer and early fall. During their period of vegetation domination, these species cover about 95% of the surface. A number of other herb species are present but only sparsely distributed. There is no moss stratum present.

Lacustrine Marsh

This marsh is situated on the northwestern shore of Wakomao Lake (approximately 360 ha). During 1993, the water table was below the peat surface; however, in 1994, this site was flooded with water possibly due to beaver dams or constructed dams blocking the outflow(s) of the adjacent lake. Water flows into this lake via a creek from a northern drainage basin (approximately 7800 ha) as well as from an approximately 300 ha artesian well area to the southwest. Water leaves Wakomao Lake through a creek at the southern tip. The lake receives secondarily treated wastewater from Clyde (population < 1000) each spring and additional nutrients from agricultural run-off. No moss and shrub strata exist and the vascular vegetation layer is dominated by *Carex aquatilis* Wahlenb., *C. rostrata* Stokes and *C. atherodes* Spreng. (an approximate cover of 95%). Also, *Typha latifolia* L. flourishes at the lake shore and *Scirpus microcarpus* Presl., *Galium labradoricum* Wieg. and *Hippuris vulgaris* L. comprise the remaining 5% of cover. The peat depth is 1.5-1.75 m and the pH of the surface water ranged from 7.1 to 8.1.

Methods

Production measurements

Mosses

Clymo's (1970) cranked wire method was employed to measure the moss growth in the bog and the ORF. Two 5 by 50 m

($250\ m^2$) plots were established in the bog in early June 1991 to determine the growth and production of the dominant moss species, *Sphagnum fuscum* (Szumigalski & Bayley, under review). Five randomly placed circular transects of 20 wires, placed about 5 cm apart, were established in each plot (a total of 200 wires). Due to the smaller dimensions of the ORF, only one plot of 5 by 25 m ($125\ m^2$) was established in June 1993. It was determined that *Sphagnum warnstorfii* and *Aulacomnium palustre* were the two dominant species in this site; therefore, three circular transects of 20 wires were set up for each moss species (60 wires per species). Growth in length was measured four times during each growing season, which was estimated to begin on the first of May and end in mid-October each year, in both sites. To convert the linear growth increments (cm/year) to production values ($g/m^2/year$), the mass per unit length per surface area (g/cm/year) was required. This was determined by extracting five cores of 85 cm^2 surface area in early October of 1993 and 1994 for each of the species measured for growth and production. The number of individual stems in each core was counted and the top 4 cm of each plant was cut off from the remainder of the plant, dried at 60 ^{o}C and weighed to the nearest 0.01 g. Since the capitulum of *Sphagnum* spp. does not change significantly during the growing season (Rochefort et al., 1990), it was removed before drying and weighing. The dry weight of each core was then converted to an average weight per 1 cm of stem per square meter ($g/cm/m^2$) for each moss species. The production values were obtained by multiplying these values by the yearly measured length increments from the cranked wires (cm/year).

Since the peat surface within the ORF and the bog are not perfectly flat, the calculated production values were corrected for hummock elevations by multiplying the production values by a correction factor which depends directly on the peat surface at each site. To estimate the actual peat surface area per vertically projected area, a 2500 cm^2 quadrat was set up into a grid of 25 equal 100 cm^2 squares. This was accomplished by stringing wires across the quadrat and the result were 36 evenly spaced grid nodes on the quadrat surface. At each circular sample transect, this quadrat was leveled and the distance from each grid node to the peat surface was measured (cm). The coordinates (x, y) of all grid nodes in association with the depths to the peat surface (z) could then the used by the computer program MacGridzo to calculate the surface area within each quadrat. This procedure was carried out at the ten and six circular transects in the bog (Szumigalski & Bayley, under review) and ORF, respectively. The average ratio of actual peat surface area to vertical projected area was then determined for both sites and the calculated moss production values were multiplied by the corresponding site correction factor to arrive at the actual moss production figure (g/m^2/year) (Table 2.1.).

The lacustrine sedge fen had very few hummocks and Clymo's cranked wire method for determining moss production could not be applied here. Instead, moss production was determined by multiple harvests of the moss mat. A 0.25 by 0.25 m (0.0625 m^2) quadrat was employed to extract five samples of the dominant moss species, *Drepanocladus aduncus*, three times during both growing seasons. From each harvested quadrat, a sub-sample of 25 moss plants was taken and the ratio of the mass of new growth, as estimated from the colour change, to the total biomass of the sample was determined (*cf.* Vitt & Pakarinen, 1977; Vasander, 1982). To estimate the total moss production per harvested quadrat, the ratio of new growth to total weight was multiplied by the total harvested moss weight per quadrat. All samples were dried at 60 ^{o}C before weighing. The sample period with the peak biomass was used as an estimate of the total NPP.

Herbs and shrubs

These two vegetation layers were measured in two 5 by 50 m (250 m^2) plots. These were established in early May (bog, ORF, LSF, RM and LM) or early June (RSF) in 1993 and ran parallel to the plots used to measure moss production within the applicable sites. Due to the smaller area available in the ORF, the two plots were 5 by 25 m (125 m^2) each. The vascular vegetation was harvested three times during each growing season, in late June, late July and late August.

Ten 0.50 by 0.50 m (0.25 m^2) randomly placed quadrats (five per plot) were clipped during each harvest period. The bog was added as a sixth study site in 1994; therefore, no vascular plant production values are available for the 1993 growing season.

All herbaceous plant material was clipped at the ground level during each sample period, dried at 48 °C and sorted into live and dead plant matter. The dead plant matter was discarded and the live plant material was further separated into individual taxa and then weighed. The maximum aboveground herb production for each site was estimated by using the month (June, July or August) with the peak live standing crop.

Shrub NPP was determined similarly to herb production with the exception that shrubs are evergreens or deciduous with secondary growth (radial growth). The radial growth plus the new terminal growth (leaves, flowers, new twigs) is an approximate estimate of the aboveground annual NPP. Radial production for *Salix* spp., *Betula* spp. and *Ledum* spp. were estimated from Szumigalski & Bayley (under review) and incorporated into the total NPP for the bog, LSF and ORF before statistical analyses were carried out. The radial production of dwarf shrubs is believed to be minimal (Vasander, 1982) and was not determined.

To estimate total vascular plant aboveground NPP, the August herb and shrub total biomass from each quadrat was combined and then statistically analyzed for differences in vascular plant production between years, sites and transects within sites.

Trees

The only site with a significantly developed tree canopy was the bog (*Picea mariana*). Since the climatic data between 1991 and 1994 were similar in average temperature, total precipitation and growing degree days on a per annum basis, I adopted the tree NPP values as determined by Szumigalski & Bayley (under review) in my analyses.

Statistical analyses

Randomized nested-block ANOVA designs were used to analyze the vascular (herbs, shrubs and trees) and the total production (herbs, shrubs, trees and mosses) separately within each site (n=10/site). In addition, fens (n=3, 10 samples/fen) and marshes (n=2, 10 samples/marsh) were combined into peatland "types" and analyzed for differences in vascular and total plant NPP using the same ANOVA design. After significance was detected in the ANOVA procedures, Tukey significant difference tests were performed. Furthermore, t-tests were used to detect significant differences among the sites between years.

Since I only examined one bog, proper replication is absent and the problem of pseudo-replication arises due to multiple sampling events within this site. Therefore, I will only attempt to prove my hypotheses for the six peatlands I am examining as part of this study and I will not make any generalizations regarding potentially similar trends for other peatlands. All statistical analyses were performed on SAS (SAS Institute Inc., 1989).

Results and discussion

Moss production

Moss species were present in three of the sites. In these sites, there were generally more differences in moss production between years than there were among sites. Of those sites with a moss stratum, the lacustrine sedge fen (LSF) had the lowest moss production in 1993 (27 g/m^2/year) and 1994 (121 g/m^2/year) (Figure 2.2.). The open rich fen (ORF) and the bog had values of 52 and 287 g/m^2/year and 156 and 268 g/m^2/year in 1993 and 1994, respectively. The moss production was significantly different ($p < 0.05$) among the sites in 1993 and although there was no significant difference ($p > 0.05$) between the bog and the ORF in 1994, together, they were significantly different from the LSF. In all sites with a moss stratum, the moss production was significantly ($p < 0.05$) lower in 1993 than in 1994.

A trend of significantly different moss production between years was previously reported by Wallén et al. (1988), Moore (1989), Rochefort et al. (1990), Francez (1992) and Szumigalski & Bayley (under review). Also, other studies showed small differences in moss production among a variety of peatlands within the same year (Rochefort et al., 1990; Szumigalski & Bayley, under review). These latter studies were conducted in several minerotrophic and ombrotrophic peatlands in Ontario and along a bog - extreme-rich fen gradient in central Alberta, respectively. Bartsch & Moore (1985) also found similar trends in poor, rich and transitional fens in Canada's sub-arctic regions.

The bog had a mean moss production of 212 g/m^2/year in 1993 and 1994 (Figure 2.2.). This value is higher than production values reported by Rochefort et al. (1990) (132 to 141 g/m^2/year in Ontario bogs), Szumigalski & Bayley (under review) (154 g/m^2/year in the same bog) and Reader & Stewart (1972) (55 g/m^2/year in a Manitoba lagg). However, my values are lower than those of Grigal (1985), who measured moss production over a three year period in Minnesota bogs (320 to 380 g/m^2/year).

Moss production in the ORF was 95 g/m^2/year in 1993 and 482 g/m^2/year in 1994, a five-fold increase (Figure 2.2.). Szumigalski & Bayley (under review) reported values of 115 to 170 g/m^2/year for an adjacent wooded moderate-rich fen in 1991 and 1992, respectively.

The mean moss production in the LSF in 1993 and 1994 was 73 g/m^2/year (Figure 2.2.), which is similar to results reported by Szumigalski & Bayley (under review) (mean of 43 g/m^2/year in the same site during 1991 and 1992). However, moss production increased 4.5-fold from 27 to 121 g/m^2/year during the years of my study. Reader & Stewart (1972) also reported similar production values for a boreal rich fen lagg in southeastern Manitoba.

The riverine marsh (RM) and the lacustrine marsh (LM) did not have a moss stratum during the years of my study.

Grigal (1985) also determined that moss growth in hollows is greater than on hummocks. I assume that moss growth is fairly uniform within the bog and the ORF since they consist primarily of hummocks. Therefore, no adjustments have to made to account for Grigal's (1985) microtopographical difference in moss growth. Furthermore, moss production in the LSF was based on a hollow species. Grigal (1985) claims that moss production values attained via the cranked wire method may underestimate the actual moss production. However, I am confident that my moss production values are truthful.

Herb production

The peak herb standing crops (maximum net primary productivity) were significantly different ($p < 0.05$) among the sites. The sequence from maximum to minimum mean peak herb production of the sites was as follows: LM > RSF = RM > LSF = ORF > bog (Figure 2.3.). The peak herb production was attained during the month of August in most sites, except the RM (July), during both growing seasons. The peak herb crop was greater in 1994 than in 1993, except for the RM, where this trend was reversed. The greatest increase (285%) in total herb production was observed in the LSF (from 80 $g/m^2/year$ in 1993 to 300 $g/m^2/year$ in 1994). Conversely, the RM exhibited the greatest decrease (58%) in total herb production (from 349 $g/m^2/year$ in 1993 to 201 $g/m^2/year$ in 1994).

The bog had the lowest herb production (34.5 $g/m^2/year$) of all six sites (Figure 2.3.). This value is higher than Szumigalski & Bayley's (under review) findings, who reported a mean value of 11 $g/m^2/year$ for the same site in 1991 and 1992. However, my values are similar to Grigal et al. (1985) and Vasander (1982), who reported values of 22 $g/m^2/year$ in a perched bog in Minnesota and 30 to 40 $g/m^2/year$ in a bog in Finland, respectively.

All fens and marshes in this study exhibited higher peak herb production values (158 to 409 $g/m^2/year$) than the bog (Figure 2.3.). Szumigalski & Bayley (under review) found values of 52 to 203 g/m^2/year in rich fens in Alberta, Bartsch & Moore (1985) reported herb production values of 90 to 233 g/m^2/year in sub-arctic fens, and Reader & Stewart (1972) measured herb production to be 164 g/m^2/year in a *Carex rostrata* and *Calamagrostis canadensis* dominated wetland in Manitoba. However, Reiners (1972) reported values of only 50 g/m^2/year in a marginal fen in Minnesota. In contrast, my fen herb production values are lower than the lower latitude sedge wetlands of Bernard & Gorham (1978) (340 to 1,500 g/m^2/year). Szumigalski & Bayley (under review) previously studied the LSF in 1991 and 1992 and reported peak herb production values of 122 and 203 g/m^2/year (mean of 163 g/m^2/year). These values are similar to my results of 80 to 300 g/m^2/year in 1993 and 1994 (mean of 190 g/m^2/year).

The lacustrine marsh (757 g/m^2/year) had significantly ($p < 0.05$) higher mean herb production values than the riverine marsh (345 g/m^2/year) for both years of this study (Figure 2.3.). These values are significantly lower than those of Bernard & Solsky (1977) for a sedge marsh in New York (1,078 to 1,741 g/m^2/year) and for a number of other studies reporting herb production values upwards of 1,000 g/m^2/year. Some studies of fishponds in Europe report values of up to 4,300 g/m^2/year for peak aboveground herb production (Kvet & Husak, 1978).

The measurement for aboveground net primary plant production by the harvest method can underestimate herb production due to shoot mortality, different time of peak biomass for different herb species and herbivory. It can also overestimate herb production due to overwintering of green shoots and translocation of old parts to new ones (Bernard & Gorham, 1978; Reader, 1978; Richardson, 1978; Wheeler & Shaw, 1991).

Shrub and tree production

Shrub aboveground production decreased along the bog - fen gradient; however, no shrub statum was present in the RSF, RM and LM (Figure 2.4.). The total shrub net primary production varied significantly ($p < 0.05$) among the sites which exhibited a shrub statum (14.3 to 126 g/m^2/year). The order of these sites from greatest to least shrub production was bog > ORF > LSF. Shrub production was not significantly different in any site between 1993 and 1994 ($p > 0.05$).

Shrub NPP in the bog was 126 g/m^2/year (sampled only in 1994) (Figure 2.4.). This value was higher than Szumigalski & Bayley's (under review) findings of 77 to 97 g/m^2/year in the same bog and Reader & Stewart's (1972) value of 53 g/m^2/year in a bog forest. However, my findings were lower than Reader & Stewart's (1972) total shrub NPP values of 308 and 241 g/m^2/year for an open bog and a sparsely treed muskeg, respectively, in Manitoba. Grigal et al. (1985) also reported a higher shrub production value for a raised bog in Minnesota (200 g/m^2/year).

The minerotrophic sites which exhibited a shrub stratum had a range of mean production values of 14 to 41 g/m^2/year for the ORF and LSF, respectively (Figure 2.4.). These values are significantly ($p < 0.05$) lower than those of a wooded rich fen investigated by Szumigalski & Bayley (under review) (152 g/m^2/year), a moderate-rich fen in Manitoba (Reader & Stewart, 1972) (458 g/m^2/year) and Richardson et al.'s (1976) fens in Michigan (338 g/m^2/year). However, my findings are similar to those of Bartsch & Moore's (1985) values of 43 to 71 g/m^2/year for a fen in Quebec.

Szumigalski & Bayley (under review) reported shrub production values ranging from 6 to 9 g/m^2/year in the LSF in 1991 and 1992. These values are similar to my findings for the two growing seasons following their study.

The RSF, RM and LM had no shrub stratum, possibly due to high water tables in these sites which may inhibit seed germination of woody plants. The raised water table decreases the oxygen transfer to seedlings and roots, resulting in the reduction in vegetative and reproductive growth and often death (Kozlowski et al., 1991).

My estimates for shrub net primary production may be low because the current year's leaves and stems may continue to grow until October (Backéus, 1985) (my last harvest was conducted in late August). Furthermore, losses due to translocation, litter fall and herbivory may decrease estimates of shrub NPP throughout the growing season as well.

Only the bog exhibited a tree stratum and NPP values from this layer were adopted from Szumigalski & Bayley (under review), who studied the same site in 1991 and 1992 (27 g/m^2/year). *Picea mariana* estimated aboveground biomass (592 g/m^2) and production (27 g/m^2/year) were lower than findings by Reader & Stewart (1972) who measured total aboveground biomass (368 g/m^2) and production (58 g/m^2/year) in a Manitoba muskeg. Bogs in Minnesota had consistently higher biomass and production values than the bog in this study. Grigal et al. (1985) determined values of 3,100 g/m^2 and 100 g/m^2/year of biomass and production, respectively, in a raised bog, and 10,000 g/m^2 and 310 g/m^2/year for the same parameters in a perched bog.

Vascular plant production (excluding trees)

A significant ($p < 0.05$) difference in aboveground vascular plant production (excluding trees) was apparent among sites and between years (1993 < 1994). The sites ranked as follows (from highest to lowest NPP): LM > RM = RSF > ORF = LSF in 1993 and LM > RSF > LSF > ORF = RM > bog in 1994. The lacustrine fens (ORF and LSF) and the bog had the lowest herb and shrub production combined (1993/94 mean), whereas the riverine fen (RSF) and both marshes (RM and LM) had the highest. Herb production increased from the bog to the fens to the eutrophic marshes (Figure 2.3.), and shrub production decreased along the same gradient (Figure 2.4.). Total vascular plant production values ranged from 94 (LSF in 1993) to 933 (LM in 1994) g/m^2/year (Figure 2.5.).

A detailed list of the taxa that comprise the herb and shrub strata is available in Appendices two & three.

Total plant production

Total mean aboveground plant production, including trees, shrubs, herbs and mosses, for all sites does not seem to increase along the bog - fen - marsh gradient in central Alberta (Figure 2.6.). From most to least productive sites, the study sites rank as follows: LM > RSF > Bog = ORF = RM > LSF. The LM had the highest mean aboveground plant production (757 $g/m^2/year$), followed by the RSF (409 $g/m^2/year$), and the LSF had the lowest mean plant production at 277 $g/m^2/year$.

Total NPP in the bog was 390 $g/m^2/year$ during the 1994 growing season. This value is higher than plant production values reported by Szumigalski & Bayley (under review) for the same site during the 1991 and 1992 growing seasons (mean of 273 $g/m^2/year$). Reader & Stewart (1972) reported total NPP values of 342 and 371 $g/m^2/year$ in a muskeg and an open bog in Manitoba, respectively. In contrast, Farrish & Grigal (1988) reported a total NPP value of 755 $g/m^2/year$ in a perched bog in Minnesota and Wieder et al. (1989) measured a total NPP of 1,045 $g/m^2/year$ in a bog in West Virginia. Both of their findings are substantially higher than my value. A latitudinal gradient of aboveground net primary plant production seems to be present for bogs, with lower NPP at higher latitudes and higher NPP at more southerly locations (Table 2.2.). European bogs are generally less productive compared to North American ombrotrophic systems as indicated by Vasander (1982), who measured 238 $g/m^2/year$ in a Finnish raised bog. However, Forrest & Smith (1975) determined that the NPP ranged from 285 to 653 $g/m^2/year$ in British blanket bogs.

The fens mean total aboveground plant production ranged from 277 to 409 $g/m^2/year$ (Figure 2.6.). These values are higher than those reported by Bartsch & Moore (1985) for sub-arctic patterned fens (114 to 335 $g/m^2/year$); they are comparable to the Michigan fens studied by Richardson et al. (1976) (341 $g/m^2/year$) and the Alberta fens examined by Szumigalski & Bayley (under review) (167 to 388 $g/m^2/year$) in 1991 and 1992. A latitudinal gradient of NPP seems to exist for fens as well. However, this gradient of increasing NPP with decreasing latitudes does not appear to be as pronounced as it is with the bogs in North America (Table 2.2.). Factors other than climate, such as hydrology, may be influencing NPP in fens.

The riverine sedge fen (RSF) was the most productive fen (409 g/m^2/year), whereas the lacustrine sedge fen was the least productive fen (277 g/m^2/year) (Figure 2.6.). Szumigalski & Bayley (under review) examined the same lacustrine sedge fen (their 'sedge fen') in 1991 and 1992 and measured a mean NPP of 214 g/m^2/year. This is significantly lower than my mean NPP for the two years following their study. This site underwent significant changes to its hydrological regime during the early 1990s, which may explain this difference in NPP (121 and 433 g/m^2/year in 1993 and 1994, respectively). The water table began to drop in 1990 (Szumigalski & Bayley, under review) and then began to rise again in 1994. This is directly correlated with the changes in NPP observed over this time period in this site. The LSF is dominated by *Carex lasiocarpa* , *C. diandra* and *C. rostrata* and Verhoeven et al. (1983) and Wheeler & Shaw (1991) reported NPP values of 210 to 250 g/m^2/year in fens with a similar vegetation composition in Europe.

The lacustrine and riverine marshes exhibited mean NPP values of 757 and 323 g/m^2/year, respectively, during the 1993 and 1994 growing seasons. These values for southern boreal marshes are low compared to findings by van der Valk & Davis (1978) (1,066 and 2,297 g/m^2/year in an Iowa prairie pothole), Bray et al. (1959) (1,680 g/m^2/year in a Minnesota marsh), Bray (1963) (1,360 g/m^2/year in another Minnesota marsh) and Auclair et al. (1976) (914 g/m^2/year in a marsh in Quebec). Furthermore, studies by Mason & Bryant (1975) and Anderson (1976) showed NPP values of European marshes to be 1,445 g/m^2/year in Norfolk, England, and 1,400 g/m^2/year in Denmark, respectively. However, all of these studies were conducted in marshes at lower latitudes and a gradient of increasing NPP with decreasing latitudes exists for marshes as well (Table 2.2.). As with fens, climate is not the only factor influencing NPP in these peatlands, but hydrology, specifically water levels (Mitsch & Gosselink, 1993) and the dominant vegetation (van der Valk & Davis, 1978) influence NPP in marshes as well.

Conclusion

I have examined five peatlands in 1993 and an additional sixth in 1994 in central Alberta, Canada. They were a bog, an open rich fen (ORF), a lacustrine sedge fen (LSF), a riverine sedge fen (RSF), a riverine marsh (RM) and a lacustrine marsh (LM).

My hypothesis of increasing net primary plant production along this bog - fen - marsh gradient was only partially supported by my findings. The total aboveground NPP increased from bogs to marshes; however, the bog did not exhibit a significantly lower NPP than the fens in this study. In fact, the LSF was significantly less productive, on average, than the bog.

The bog exhibited a NPP of 390 g/m^2/year in 1994 and this value is intermediate for bogs in North America. The fens had NPP values ranging from 277 to 409 g/m^2/year, which is also intermediate for North American fens; however, the marshes of this study were significantly less productive than other North American marshes (323 to 757 g/m^2/year). The bogs and fens complement a latitudinal gradient with NPP increasing with decreasing latitudes. Production values of marshes differ considerably, depending on the dominant vegetation of the marsh (van der Valk & Davis, 1978), but a similar, although not as prominent, latitudinal gradient is present as well (Table 2.2.).

Moss and shrub production decreased along this bog - fen - marsh gradient in central Alberta, whereby herb production increased along the same gradient. Trees were found only in the bog and their NPP was small compared to the production of the other vegetation stata. Shrub and moss strata were absent in both marshes. Moss and herb production was more variable between years than among sites, whereas shrub production remained similar during both years of this study. Generally, all sites had a greater total aboveground NPP in 1994 than in 1993 (except the riverine marsh, whose water was blocked by beaver dams).

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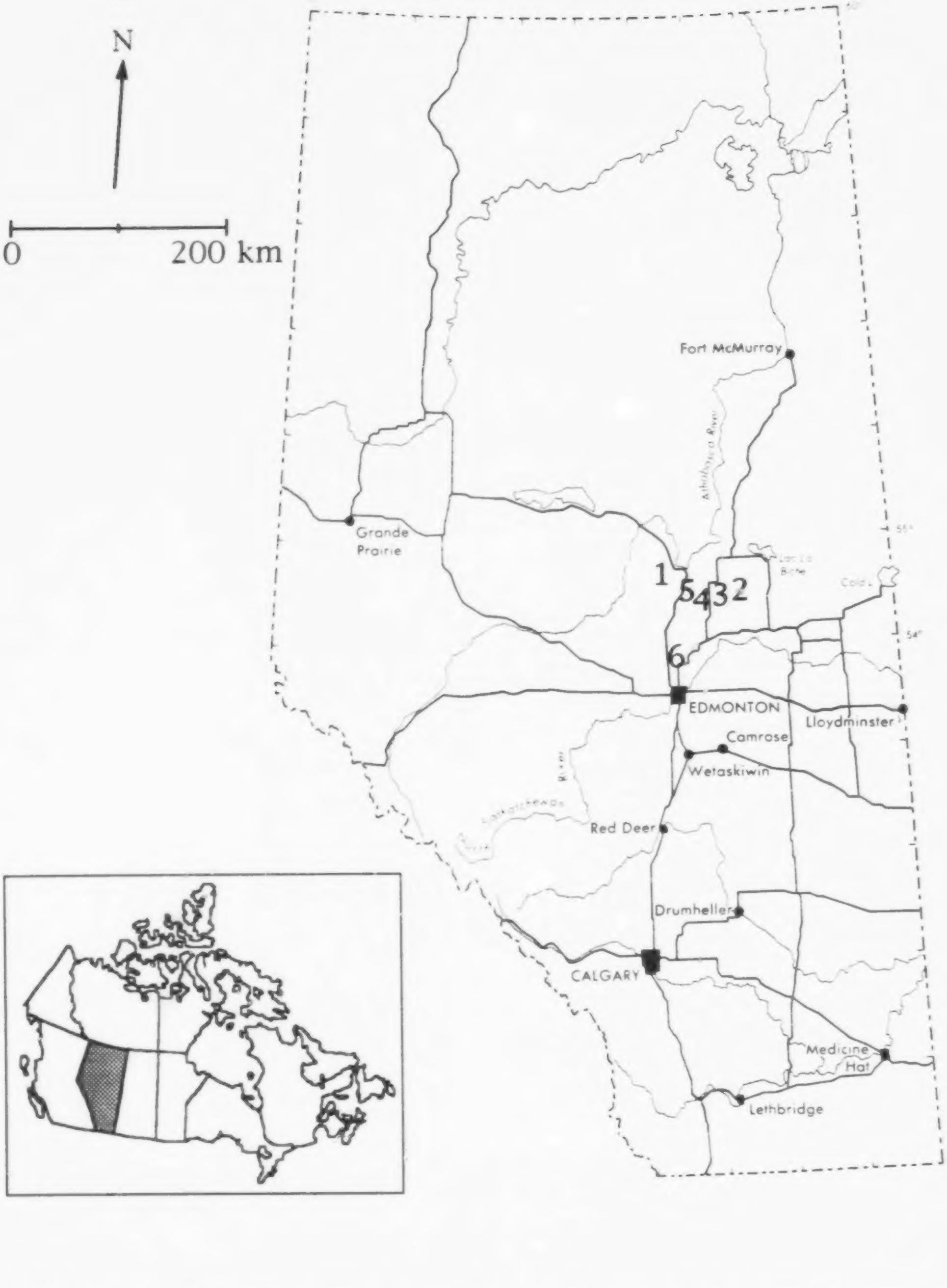
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Camrose
Wetaskiwin
Red Deer
Drumheller
CALGARY
Medicine Hat
Lethbridge

Figure 2.1. Relative location of the peatlands in central Alberta (**1** = bog, **2** = open rich fen, **3** = riverine sedge fen, **4** = lacustrine sedge fen, **5** = riverine marsh and **6** = lacustrine marsh).

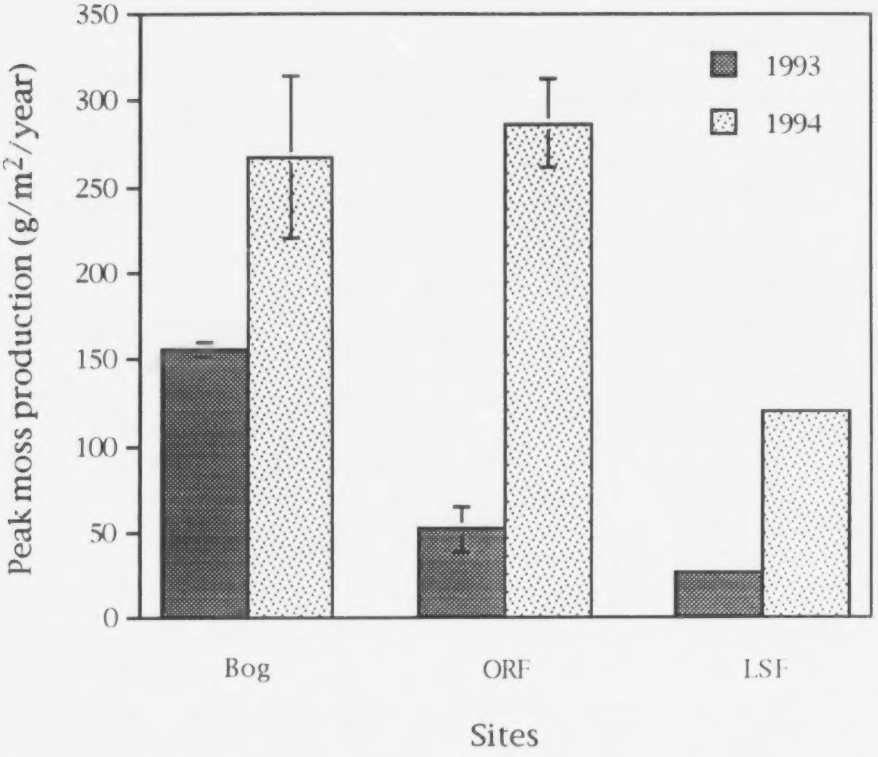

Figure 2.2. Comparison of moss production (mean +/- SE) assuming 100% cover of the ground layer by the dominant species in three peatlands (bog, ORF = open rich fen, LSF = lacustrine sedge fen) in 1993 and 1994. No significant moss stratum was present in the riverine sedge fen and it was absent in the riverine and lacustrine marshes. SE < 2.5 $g/m^2/year$ at columns without error bars.

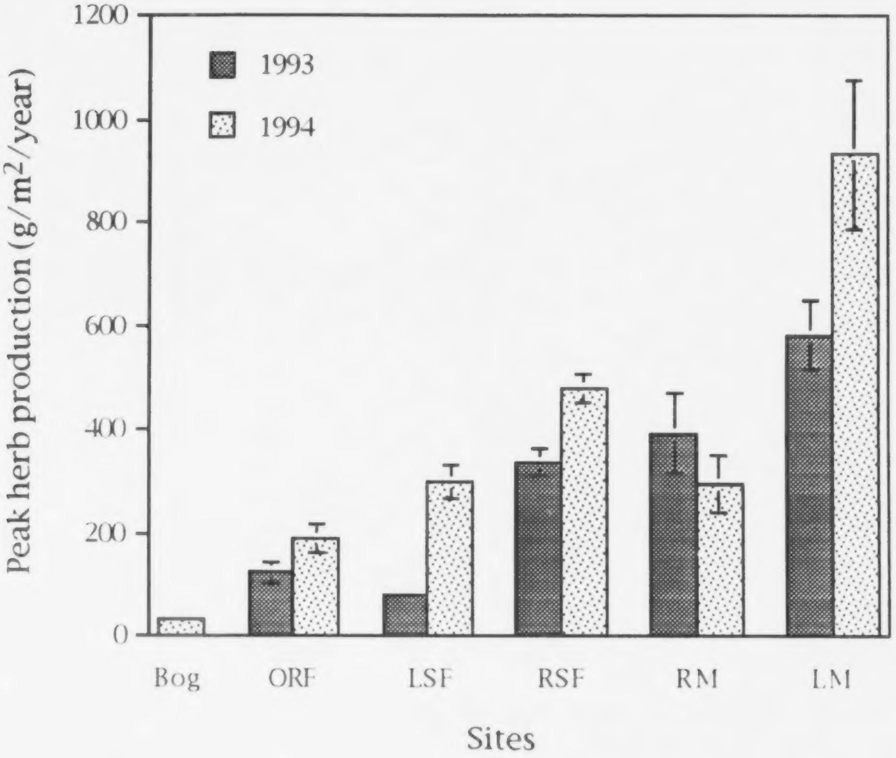

Figure 2.3. Comparison of aboveground peak herb production (mean +/- SE) in six peatlands (bog, ORF = open rich fen, LSF = lacustrine sedge fen, RSF = riverine sedge fen, RM = riverine marsh, LM = lacustrine marsh) in 1993 and 1994. The bog was sampled only in 1994. SE < 10 g/m^2/year at columns without error bars.

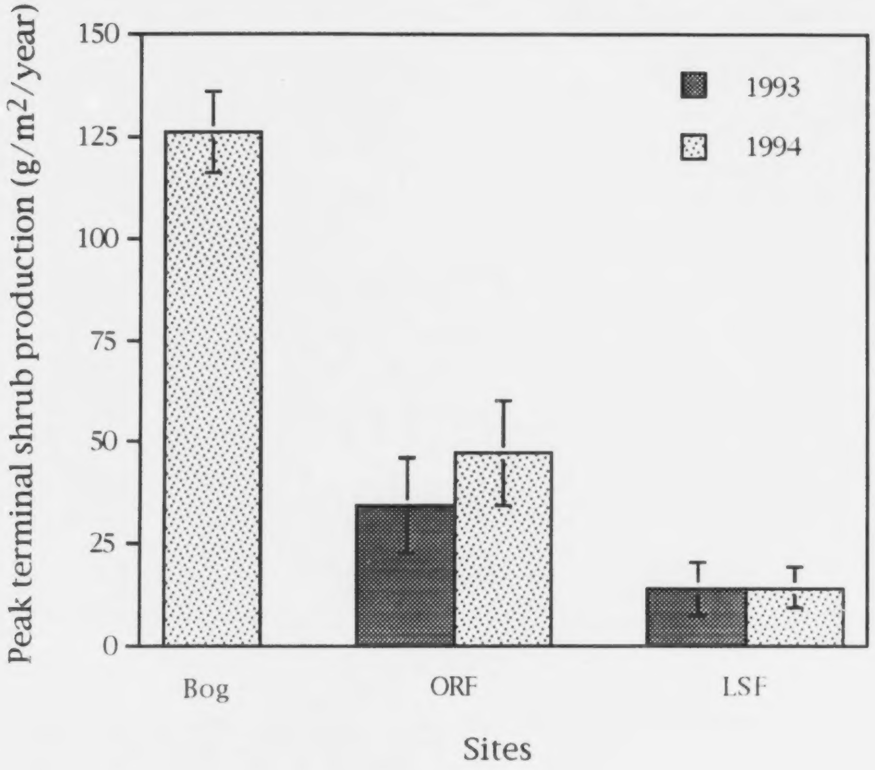

Figure 2.4. Comparison of peak aboveground terminal shrub production (mean +/- SE) in three peatlands (bog, ORF = open rich fen, RSF = riverine sedge fen) in 1993 and 1994. The bog was sampled only in 1994 and no shrub stratum was present in the lacustrine sedge fen and the riverine and lacustrine marshes.

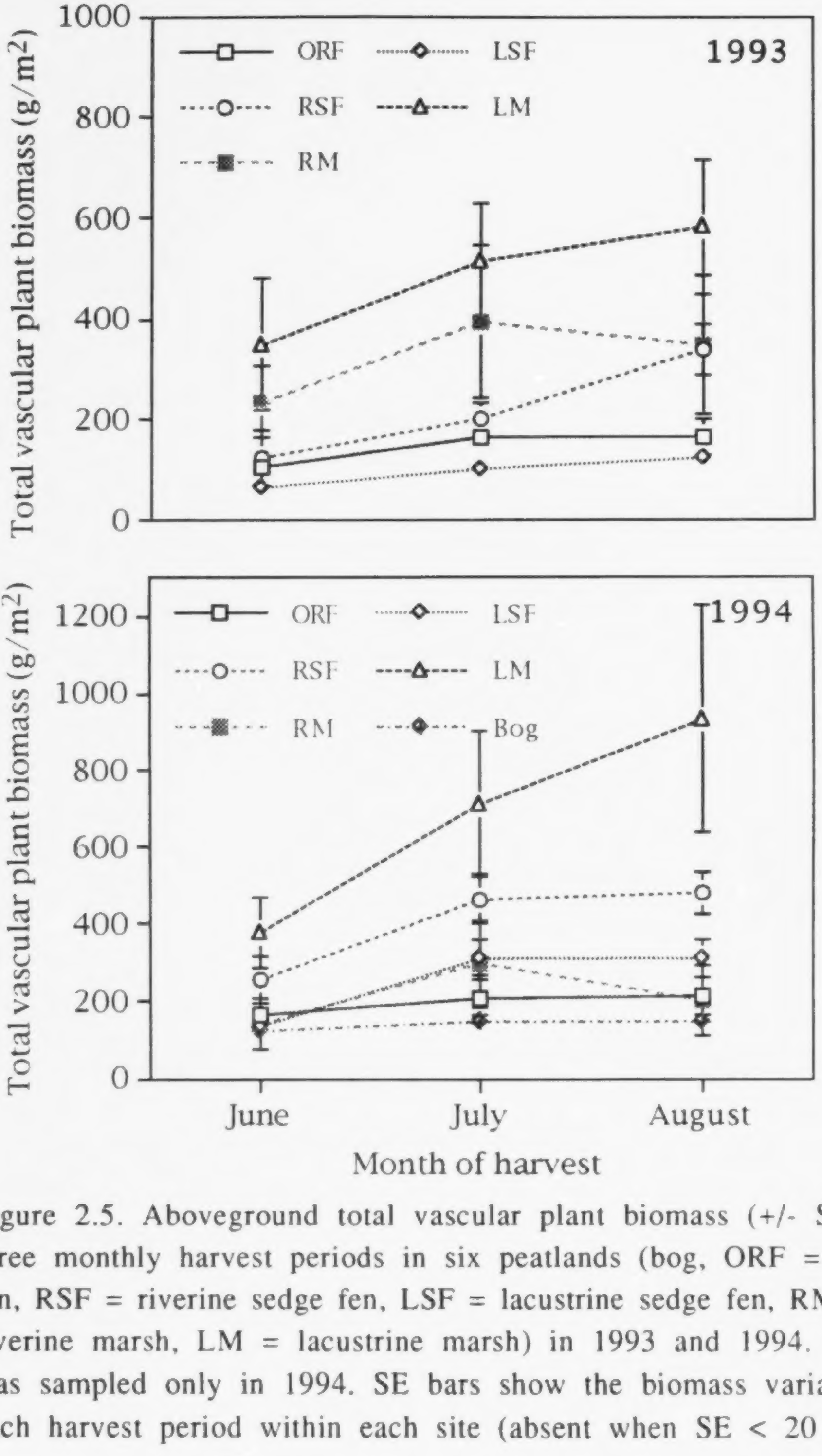

Figure 2.5. Aboveground total vascular plant biomass (+/- SE) at three monthly harvest periods in six peatlands (bog, ORF = open rich fen, RSF = riverine sedge fen, LSF = lacustrine sedge fen, RM = riverine marsh, LM = lacustrine marsh) in 1993 and 1994. The bog was sampled only in 1994. SE bars show the biomass variation at each harvest period within each site (absent when SE < 20 g/m^2).

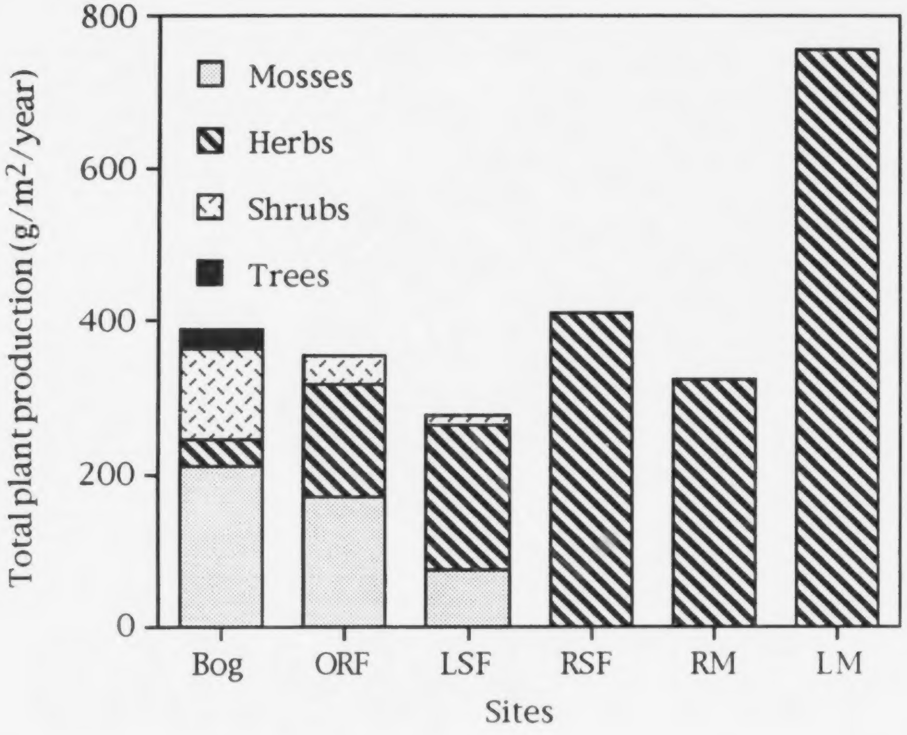

Figure 2.6. Comparison of total aboveground plant production in six peatlands (bog, ORF = open rich fen, RSF = riverine sedge fen, LSF = lacustrine sedge fen, RM = riverine marsh, LM = lacustrine marsh). Bars represent the mean of 1993 and 1994, except for tree production (where applicable) which is based on Szumigalski & Bayley (under review). The bog was sampled only in 1994.

Table 2.1. Growth and net primary plant production of moss species in three peatlands in 1993 and 1994. Bulk density is in grams per centimeter per square meter, growth is in centimeters and production is in grams per square meter per period.

Site/Species	**Bulk Density**	**Surface area correction factor**	**1993 May - October growth**	**1993 May - October production**	**1994 May - October growth**	**1994 May - October production**
Bog	474	1.09 *				
Sphagnum fuscum			0.38	155.9	0.65	267.8
ORF	92	1.11				
Sphagnum warnstorffii			0.54	33.2	4.46	275.3
Aulacomnium palustre			0.72	136.2	2.15	404.7
LSF	419	1.01				
Drepanocladus aduncus			0.26	26.8	1.18	120.8

* = adopted from Szumigalski & Bayley (under review)

Table 2.2. Aboveground net primary plant production (g/m^2/yr) of different strata and totals for North American peatlands in order of decreasing latitude. Columns may not add up to totals due to rounding.

Wetland type	Lacation and Source	Latitude	Moss	Herb	Shrub	Tree	Total
Bogs							
Bog	Alberta Szumigalski & Bayley (under review)	54° 41' N	155	11	87	27	280
	This study		212	34	117	* 27	390
Muskeg	Manitoba Reader & Stewart (1972)	49° 53' N	17	--	267	58	342
Bog	Manitoba Reader & Stewart (1972)	49° 53' N	55	--	308	** 8	371
Raised bog	Minnesota Grigal et al. (1985)	47°- 48°N	320	14	200	100	634
Perched bog	Minnesota Grigal et al. (1985)	47° 30' N	380	22	43	310	755
Bog	West Virginia Wieder et al. (1989)	39° 07' N	449	209	387	--	1,045
Fens							
Poor fen	Quebec Bartsch & Moore (1985)	54° 43' N	38	27	49	--	114
Rich fen	Quebec Bartsch & Moore (1985)	54° 43' N	41	233	61	--	335
Transitional fen	Quebec Bartsch & Moore (1985)	54° 43' N	39	90	47	--	176
Poor fen	Alberta Szumigalski & Bayley (under review)	54° 41' N	123	54	134	--	310
Open rich fen	Alberta This study	54° 28' N	170	148	38	--	356
Wooded moderate-rich fen	Alberta Szumigalski & Bayley (under review)	54° 28' N	142	65	108	44	360
Sedge fen	Alberta Szumigalski & Bayley (under review)	54° 28' N	43	163	8	--	214
Lacustrine sedge fen	Alberta This study	54° 28' N	74	190	13	--	277
Riverine sedge fen	Alberta This study	54° 28' N	--	409	--	--	409
Extreme-rich fen	Alberta Szumigalski & Bayley (under review)	53° 42' N	149	89	6	--	245
Lagg	Manitoba Reader & Stewart (1972)	49° 53' N	76	***300	***650	--	1,026
Marginal fen	Minnesota Reiners (1972)	45°N	--	49	6	655	710
Leather leaf-bog birch fen	Michigan Richardson et al. (1976)	44°N	--	3	338	--	341

Marshes							
Riverine marsh	Alberta This study	54° 28' N	--	323	--	--	323
Lacustrine marsh	Alberta This study	54° 28' N	--	757	--	--	757
High fluctuating water table marsh	Minnesota Bray (1963)	45° N	--	1,360	--	--	1,360
Prairie pothole marsh ****	Iowa van der Valk & Davis (1978 a)	42° N	--	2,297	--	--	2,297
Prairie pothole marsh *****	Iowa van der Valk & Davis (1978 a)	42° N	--	2,858	--	--	2,858
Typha spp. marsh	New Jersey Jervis (1969)	41° N	--	1,905	--	--	1,905
Low fluctuating water table marsh	South Carolina Boyd (1971)	33° N	--	530 - 1,132	--	--	530 - 1,132

* = estimated from Szumigalski & Bayley (under review)
** = estimated from Reader & Stewart (1972)
*** = production of strata estimated from data
**** = Typha glauca dominated
***** = Carex atherodes dominated

3. DECOMPOSITION ALONG A MODERATE-RICH FEN - MARSH GRADIENT IN BOREAL ALBERTA.

Introduction

Peatlands are ecosystems which are, in part, defined as having a peat thickness of at least 30-40 cm (Gorham, 1991). Various authors have suggested that peat accumulation is the result of slow litter decomposition rather than rapid net primary production (Clymo, 1965; Malmer, 1986; Farrish & Grigal, 1988; Vitt, 1990). Since peat is accumulating on an annual basis, peatlands are important components in the global carbon cycle. Their importance is further enhanced by the fact that peatlands cover a significant area of the boreal and sub-arctic regions of the northern hemisphere (Gorham, 1991).

Decomposition is a complex process which includes nearly all changes in organic matter that has undergone senescence or death (Brinson et al., 1981). Leaching of soluble organic matter precedes losses due to the assimilation by micro-organisms or removal by animals. Decomposition is completed with the loss of physical structure and changes in the chemical constituents of the remaining organic matter (Clymo, 1983). The rate of decomposition is affected by moisture, anoxia, temperature, acidity and the nutrient status of ecosystems (Brinson et al., 1981; Bartsch & Moore, 1985; Farrish & Grigal, 1988; Gorham, 1991). Litter quality also affects the rate of decomposition (Brinson et al., 1981; Bridgham & Richardson, 1992; Szumigalski & Bayley, under review).

Various methods have been employed in the past to assess rates of decomposition in ecosystems, including soil respiration (Bridgham & Richardson, 1992), changes in peat microstructure (Johnson et al., 1990), the degree of humification (Malmer, 1986) and the C:N ratio of the peat (Malmer & Holm, 1984). The most commonly used method involves determining the rate of weight loss of a known quantity of litter over time. Decomposition measurements using cellulose (in the form of filterpaper or cotton strips) are used in some studies to compare rates of decay between sites (Bartsch & Moore, 1985; Farrish & Grigal, 1988; Lieffers, 1988; French, 1988; Farrish & Grigal, 1988; Verhoeven et al., 1990; Santelmann, 1992; Verhoeven & Arts, 1992). Other studies have used a standard plant species inserted into the substrate of all sites (Ohlson, 1987; Johnson & Damman, 1991; Szumigalski & Bayley, under review). The technique using natural plant litter provides nutrients (N, P, K), whereas cellulose only provides carbon for decomposers.

A number of studies have examined rates of decomposition of *Sphagnum* spp. (Clymo, 1965; Bartsch & Moore, 1985; Johnson et al., 1990; Rochefort et al., 1990; Johnson & Damman, 1991; Szumigalski & Bayley, under review) but "brown" mosses have received far less attention (Reader & Stewart, 1972; Vitt, 1990; Szumigalski & Bayley, under review). Most decomposition studies of vascular plant litter have concentrated on aboveground plant material in fens and marshes (Chamie & Richardson, 1978; Bartsch & Moore, 1985; Ohlson, 1987; Verhoeven & Arts, 1992; Szumigalski & Bayley, under review) and to a lesser degree in bogs (Reader & Stewart, 1972). Few decomposition measurements have been made in southern boreal fens and marshes.

My study of decomposition processes in 1993 and 1994 included five major aspects: (1) decomposition of the dominant plant species across a fen - eutrophic marsh gradient, (2) decomposition of a standard plant species across a fen - eutrophic marsh gradient, (3) decomposition of cellulose (filterpaper) across the fen - eutrophic marsh gradient, (4) the effects of substrate quality on decomposition rates and (5) the effects of environmental parameters on decomposition rates. I hypothesize that the rates of decomposition increase along the fen - eutrophic marsh gradient for the dominant species, standard species and cellulose (filterpaper) due to increases in pH and surface water nutrients. I also hypothesize that plant tissues with a lower C:N ratio (hence a higher percent of total N) will decompose at a higher rate due to the greater nitrogen availability for decomposers and I further hypothesize that the C:N ratio of the plant litter will change significantly over time in all sites due to the mineralization of nitrogen from the plant material by microbes.

Study area and site descriptions

The five study sites which were examined in 1993 and 1994 represent the range of peatlands present in the southern boreal region of Alberta, Canada. These included an open rich fen (ORF), a riverine sedge fen (RSF), a lacustrine sedge fen (LSF), a riverine marsh (RM) and a lacustrine marsh (LM). The ORF is located at 54° 28' N, 113° 17' W), the LSF (54° 28' N, 113° 19' W) and the RSF (54° 28' N, 113° 18' W) are located east of Perryvale, while the RM is located northwest of Perryvale at 54° 28'N and 113° 23' W, and the LM is located northeast of Clyde (54° 10' N, 113° 34' W) (Figure 3.1.).

The climate of the area is characterized by mild summers and cold, snowy winters (Vitt et al., in press). The long term mean annual temperature is 1.7 °C (Environment Canada, 1982) and the total mean precipitation is approximately 500 mm for all sites. Appendix 1 summarizes the climatic data for the 1993 and 1994 growing periods for all sites. All five peatlands lie within the Boreal Forest Region of Canada (Rowe, 1972). "Brown" moss and *Sphagnum* nomenclatures follow Anderson et al. (1990) and Anderson (1990), respectively, whereas hepatics nomenclature follows Vitt et al. (1988) and that of the vascular plants follows Packer (1983).

General descriptions of the study sites are as follows:

Lacustrine Sedge Fen

This site is a large expanse of sedge dominated peatland situated aside a large body of water (approximately 62 ha) in a former north-south drainage channel (Vitt et al., in press). This fen consists of a mainly flat topography with the occasional small hummock (about 5% of the peatland surface). The lacustrine sedge fen was largely inundated with water for most of 1991, characteristic of a marsh, but began to dry out in 1992. Therefore, Vitt et al. (in press) classified this peatland as an extreme-rich fen and concluded that it may be in a transitional phase from a moderate- to an extreme-rich fen. In 1993, this fen continued to dry out but was once again flooded in 1994, possibly due to beaver dams at the outflow of the former drainage channel. The vascular vegetation consists primarily of *Carex lasiocarpa* Ehrh. and *C. diandra* Schrank, while the shrub stratum comprises only about 5% of the peatland cover and consist of *Salix pedicellaris* Pursh and *Betula pumila* L. *var. glandulifera* Regel exclusively. The moss layer is discontinuous and dominated by *Drepanocladus aduncus* (Hedw.) Warnst. and *Calliergon giganteum* (Schimp.) Kindb. in wet pools and by *Aulacomnium palustre* (Hedw.) Schwaegr. on top of dry hummocks. Szumigalski & Bayley (under review) previously studied this fen, their 'sedge' fen, in 1991 and 1992.

Riverine Sedge Fen

This peatland is part of an extensive wetland complex adjacent to the lacustrine sedge fen. It receives water from a discrete inflow at the southern end, and the outflow at the northern end controls the water table height. The water table was above the peat surface during the 1993 and 1994 growing seasons. In the spring of 1994, a small constructed dam blocked the outflow and as a result, the water table during the second growing season was substantially higher than during the previous year. The vascular vegetation stratum is dominated by *Carex aquatilis* Wahlenb., *C. rostrata* Stokes and *C. lasiocarpa* Ehrh. which comprise about 95% of the cover. Mosses are very sparsely distributed and *Drepanocladus aduncus* (Hedw.) Warnst., *Brachythecium mildeanum* (Schimp.) Schimp. *ex* Milde and *Tomenthypnum nitens* (Hedw.) Loeske are most dominant. The thalloid liverwort *Marchantia polymorpha* L. was also present.

Open Rich Fen

This fen is a floating mat surrounding a small body of water. The peat surface is a uniform carpet which fluctuates with the water table of the associated slough. The peat is approximately 1 m thick floating over 1-1.5 m of water below which an additional 1-1.5 m of peat are located. The vascular plant strata are dominated by *Carex lasiocarpa* Ehrh.. Also, *Carex diandra* Schrank, *C. rostrata* Stokes and *C. limosa* L. are present and along with the former dominant sedge species they comprise about 90% of the vegetation cover. The shrub layer consists predominantly of *Salix pedicellaris* Pursh, *Andromeda* *polifolia* L. and *Oxycoccus quadripetalus* Gilib., whereas the moss stratum is dominated by *Calliergonella cuspidata* (Hedw.) Loeske, *Hamatocaulis vernicosus* (Mitt.) Henedäs, *Sphagnum warnstorfii* Russ. and *Aulacomnium palustre* (Hedw.) Schwaegr. The latter two species comprise about 80% of the moss cover in this fen.

Riverine Marsh

This site is located on the floodplain of Tawatinaw River. During 1993, this marsh was periodically inundated with water and the water table was above the peat surface. A beaver dam just above the study area retained much of the stream flow and the water table sunk well below the peat surface in 1994. The vascular vegetation layer is dominated by *Carex aquatilis* Wahlenb., *C. rostrata* Stokes and *C. atherodes* Spreng. during spring and early summer and by *Calamagrostis canadensis* (Michx.) Beauv. and *C. inexpansa* A. Gray during late summer and early fall. During their period of vegetation domination, these species cover about 95% of the surface. A number of other herb species are present but only sparsely distributed. There is no moss stratum present.

Lacustrine Marsh

This marsh is situated on the northwestern shore of Wakomao Lake (approximately 360 ha). Water enters the lake at the northern tip (from an approximately 7,800 ha drainage basin) and from an artesian well area along the southwestern shore (approximately 300 ha). Water flows out of Wakomao Lake through a small creek at the southern tip which then drains into Redwater River. During 1993, the water table was below the peat surface, but in 1994, this site was flooded with water, possibly due to beaver dams or man made dams blocking the outflow(s) of the lake. The lake receives secondarily treated wastewater from Clyde (population < 1000) each spring and additional nutrients from agricultural run-off. No moss and shrub strata exist, and the vascular vegetation layer is dominated by *Carex aquatilis* Wahlenb., *C. rostrata* Stokes and *C. atherodes* Spreng. (an approximate cover of 95%). Also, *Typha latifolia* L. flourishes on the lake shore.

Methods

Decomposition measurements

Dominant species

Live aerial portions of the dominant vascular plant species from each site were collected in early June, 1993. These were *Carex lasiocarpa* from all five sites, additionally *Salix pedicellaris* (leaves from the upper 0.10 m of the plant) and *Typha latifolia* from the open rich fen and the lacustrine marsh, respectively. The plant material was oven-dried at 60 °C for 48 hours and 1.8-2.5 g samples were placed into pre-weighed nylon mesh bags (3 x 6 cm, 1 mm mesh gauge). These decomposition bags were sewn shut and placed horizontally just beneath the peat surface. Thirty decomposition bags per dominant plant species were deployed in each site (sixty in the open rich fen and the lacustrine marsh) and each bag was tied to a wooden stake within each site to avoid losses. After 30, 60, 100, 365 (one year) and 456 (1 1/4 years) days, six replicates from each plant species were retrieved from each site. Coarse roots and other debris were removed immediately from the bags and each decomposition bag was further cleaned from finer debris with forceps in the laboratory before drying them at 60 °C for 48 hours. Each bag was then weighed to the nearest 0.001 g.

The percent weight losses (k') over the incubation periods of 30, 60, 100, 365 and 456 days were determined using the following equation (*cf.* Reader & Stewart, 1972; Bartsch & Moore, 1985; Szumigalski & Bayley, under review):

$$k' = \{(X_0 - X)/X_0\} \ (100)$$

where X_0 represents the initial dry litter weight (g) before decomposition and X the final dry litter weight (g) after incubation in the field. The percent weight remaining (k) over the same incubation periods were determined by subtracting k' from 1.

The simple exponential decompositon model was used to estimate decay rates (Olson, 1963):

$$X/X_0 = e^{-k_{se}\,t}$$

where X and X_0 are defined as above, k_{se} is the decay constant and t is time (days). This model is believed to best describe the weight loss of plant litter over time in ecosystems (Wieder & Lang, 1982).

Standard plant species and cellulose

One standard plant species, *Carex aquatilis* from the riverine sedge fen, and cellulose (Whatman #1 filterpaper, diameter 150 mm, typical ash content 0.06%) were used to compare the rates of decomposition among all sites. The live plant litter was collected in early June 1994 and deployed along with the filterpaper in separate mesh bags within all sites on the same date as the dominant plant litter from the previous year's study. The filterpaper was folded twice in half before being placed into the decomposition bags. Bags were retrieved after 30, 60 and 100 days only, otherwise the same procedures as above were followed.

Leaching of soluble organic compounds from plant litter

Leaching of soluble organic compounds before microbial decomposition processes begin can account for a substantial weight loss (Ohlson, 1987). Since all live plant litter for these decomposition studies were collected in early summer, I have to account for this weight loss as this plant litter does not have the same nutrient quality as that which would decompose under natural conditions in the fall.

Twenty replicates of dried (at 60 ^{o}C for 48 hours) 1.5-2.5 g *Carex aquatilis* samples from the riverine sedge fen were placed into pre-weighed decomposition bags and exposed to UV-radiation for 3 hours. Ten replicates were immersed into individual 600 mL beakers containing fungicides (6.0 mL Rose Bengal, 6 mL Benlate and 4.2 g

Quintozene), antibiotics (0.064 g tetracycline hydrochloride) and 588 mL of double-distilled water (2d-H_2O). The remaining ten bags (controls) were immersed into 2d-H_2O only. Each beaker was covered with Parafilm "M" laboratory film and placed into a dark cupboard. After seven days, the samples were washed with 2d-H_2O, dried to constant weight at 60 °C and weighed to the nearest 0.001 g. The percent weight losses (k') were determined as outlined above.

Carbon, nitrogen and C:N analyses

Methods used to analyze tissue samples for carbon (C) and nitrogen (N) were followed as described by Szumigalski & Bayley (under review). Plant samples were ground and analyzed for total C and total N content using a Model 440 Elemental Analyzer (Control Equipment Corp.). Amounts were expressed as percent nitrogen (% N) and percent carbon (% C) of total dry weight and C:N ratios were determined by dividing % C by % N for each sample. The initial % C, % N and C:N were derived from means of three samples of each litter type collected. Final values of these parameters were obtained from the incubated samples within each peatland after the following days of decomposition: 30, 60, 100 (for the standard plant litter in 1994), 365 and 456 (for the dominant plant species in 1993 and 1994).

Water levels

Steven's F water level recorders were used to monitor the water table fluctuations within each site during most of the ice free season in 1993 and 1994. Additionally, manual measurements were taken from permanently attached meter sticks.

Measurements from a pore water sampler were used to determine the annual average water level relative to the peat surface within each site. These measurements were then compared to the current reading on the water level recorders and meter stick.

Water chemistry

Water samples for laboratory analyses were collected bimonthly from early May until mid-November during 1993 and 1994. All samples from each site were collected from the same location (a 25 cm deep depression within the peat), placed into a cooler during transportation and refrigerated until analyses were performed.

All samples were filtered initially with GFC filters. Samples for nitrate (NO_3^-), soluble reactive phosphorus (SRP) and total dissolved phosphorus (TDP) were re-filtered with a 0.45 µm millipore (HAWP) filter and the samples for NO_3^- and NH_4^+ were analyzed on a Technicon Auto Analyzer II within 24 hours of collection. Total phosphorus (TP), SRP and TDP were measured following the methods of Bierhuizen & Prepas (1985). Vitt et al. (in press) used the same methods.

Depth of oxidation

Measurements of oxidation depth followed the methods described by Bridgham et al. (1991). Fifteen steel welding rods of 1.0 m length were placed into each site in early May 1994, exposing only the top 0.2 m. The rods were placed within a 0.2 m^2 area of similar microtopography and three rods were collected at monthly intervals from June until October. The depths of rust relative to the peat surface were measured and the depth of oxidation was determined by calculating the mean of these monthly measurements from June to October.

Statistical analyses

ANCOVAs of the plant litters (dominant plant species, standard plant species) and the filterpaper were employed to examine the differences in weight losses among and within the peatlands. The initial weight of the plant litter was used as a covariate in these analyses.

Comparisons of weight losses of the standard plant species and the filterpaper were made to examine the differences in their weight losses across the fen - marsh peatland gradient. The filterpaper and standard species were analyzed separately within each site to test for significant differences in decomposition rates over each decomposition period (30, 60 and 100 days) and to determine significant weight loss differences between both litter types.

The weight loss of the dominant species (*Carex lasiocarpa* in all sites and additionally *Typha latifolia* and *Salix pedicellaris* in the lacustrine marsh and ORF, respectively) were tested for significant differences across the peatland gradient and each site was tested for significant differences among their decomposition periods (30, 60, 100, 365 and 456 days).

All the above listed analyses were also carried out for decomposition rates (/day) determined from the simple exponential decay model (Olson, 1963).

Multiple stepwise regressions (forward) were performed to determine which environmental parameter accounted for the greatest variation in the weight remaining of each litter type. For these analyses, fens and marshes were combined into two individual groups. An additional multiple stepwise regression was performed on all sites combined into one large peatland group.

Pearson correlation coefficients determined whether any of the environmental parameters were correlated to each other, and autocorrelation analyses were performed on individual environmental parameters to determine if successive data points of each environmental parameter within each site over time were correlated to each other.

Most statistical analyses were performed on SAS (SAS Institute Inc., 1989), except for the autocorrelation analyses, which were performed on SYSTAT (SYSTAT Inc., 1992).

Results and discussion

Decomposition of the dominant local litter

The weight loss of *Carex lasiocarpa* differed significantly ($p < 0.001$) among the sites over 456 days. Also, a significant difference in the weight loss of *Salix pedicellaris* versus *C. lasiocarpa* was detected in the ORF ($p < 0.05$), whereby *S. pedicellaris* decomposed at a slower rate than *C. lasiocarpa*. However, the rate of decomposition of *Typha latifolia* did not differ significantly from that of *C. lasiocarpa* in the lacustrine marsh over 456 days in 1993/94 ($p > 0.05$).

Overall, the weight losses of *Carex lasiocarpa* after 456 days were not significantly different from those after 365 days. However, significant differences were detected among the weight losses after 100, 60 and 30 days ($p < 0.001$) (Figure 3.2.).

Carex lasiocarpa

In the ORF, local *Carex lasiocarpa* exhibited k values (% weight remaining) of 62.4, 46.1, 42.8, 40.8 and 35.4 after 30, 60, 100, 365 and 456 days, respectively (Figure 3.2.). The rate of decomposition for this species was 0.0022 /day over 456 days. In the riverine sedge fen (RSF) and the lacustrine sedge fen (LSF), the local *C. lasiocarpa* had k values of 74.5, 63.4, 62.5, 50.2, 54.8 and 78.9, 68.8, 62.9, 41.7 and 31.5 over the same sampling periods, respectively. The rates of decomposition were 0.0013 (RSF) and 0.0025 /day (LSF) over 456 days (Table 3.1.). These fens exhibited a range of weight loss from 49.8 to 59.2% after one year (Figure 3.2.).

Szumigalski & Bayley (under review) studied the rate of decomposition of local *Carex lasiocarpa* in the same ORF during 1991 and 1992 and measured a weight loss of 50% after the first year. This represents a rate of decomposition of 0.0019 /day and is similar to my results (Table 3.1.). Also, Verhoeven & Arts (1992) examined the weight loss of a local *Carex* spp. in a floating mat fen in the Netherlands and determined a weight loss of 27 to 45% over 770 days. I calculated that their litter had lost approximately 41 to 67% of its weight after 456 days. This would represent a rate of decomposition of 0.0014 to 0.0030 /day and make their results comparable to mine as well. However, Bartsch & Moore (1985) and Ohlson (1987) studied the weight losses of *Carex* spp. in a sub-arctic fen in Quebec and in an intermediate and spring-area fen in Sweden, respectively. Their weight losses ranged from a minimum of 13.4% in the sub-arctic fen (mean weight loss of approximately 24% for four *Carex* spp., 0.0008 /day) to 44% (0.0016 /day) and 81% (0.0045 /day) in the intermediate and spring-area fens during the first year of decomposition.

The riverine marsh (RM) and the lacustrine marsh (LM) exhibited k values of 66.6, 58.9, 53.8, 44.4, 41.9 and 69.1, 55.1, 43.2, 50.6 and 27.7 over 30, 60, 100, 365 and 456 days, respectively. Marsh weight losses ranged from 43.4 to 49.4% after one year, making their rates of decomposition very similar (0.0020 /day in the RM and 0.0025 /day in the LM over 456 days) (Table 3.1.). Davis & van der Valk (1978) reported similar values for two marshes in Iowa. They found that *Carex atherodes* lost 20% of its weight after 225 days (0.0010 /day) and and 50% after 330 days (0.0021 /day).

Typha latifolia

Typha latifolia exhibited k values of 65.0, 46.0, 41.5, 36.4 and 32.7 after 30, 60, 100, 365 and 456 days (Figure 3.2.). The rate of weight loss over 456 days was 0.0025 /day (Table 3.1.). After one year, this species had lost 63.6% of its weight.

Davis & van der Valk (1978) reported a first year weight loss of 50% for *Typha glauca* in an Iowa marsh and calculated values from Nelson et al. (1990) indicate weight losses of 49% and 73% for the same species at Delta Marsh, Manitoba, after 30 and 60 days, respectively. Webster & Simmons (1978) examined *Typha latifolia* in a reservoir in Virginia and determined a rate of weight loss of 0.0104 /day over 300 days. This is substantially higher than my results. However, Boyd's (1970) and Puriveth's (1980) results are similar to my values. They reported 0.0035 /day in a pond over 180 days (Boyd, 1970) and 0.0019 /day in Theresa Marsh, Wisconsin, over 348 days (Puriveth, 1980). Conversly, Hill & Webster's (1982) decay rate of 0.0070 /day in New River, Virginia, over 56 days is considerable lower than my decay rate for the same species after 60 days.

Salix pedicellaris

In the ORF, *Salix pedicellaris* exhibited k values of 82.4, 64.6, 68.5, 58.2 and 44.9 after 30, 60, 100, 365 and 456 days, respectively (Figure 3.2.). After one year, *S. pedicellaris* had lost 41.8% of its mass (k'), a rate of decomposition of 0.0014 /day (Table 3.1.).

Bartsch & Moore (1985) reported k' values for *Salix* spp. of 13.9 to 18.2 after one year in a sub-arctic rich fen. This represents a maximum rate of decomposition of 0.0006 /day and is substantially lower than mine. However, Chamie & Richardson (1978), Mason & Bryant (1975) and Heal & French (1974) reported similar first year weight loss values. These were k' = 46 (0.0017 /day) for *Salix* leaves in a sedge and shrub bog in Michigan, k' = 30 (0.0010 /day) to 34 (0.0011 /day) for two *Salix* spp. in a lagg in Manitoba and k' = 33 (0.0011 /day) for *Salix* spp. shoots in a monocot plant species dominated bog in Norway, respectively.

Substrate quality of the dominant litter types (%C, %N, C:N)

The initial %C content of the dominant local litter ranged from 36.77% (*Salix pedicellaris*) to 39.90% (*Typha latifolia*) (Table 3.2.). Generally, the percent C content increased from these levels into the low to mid 40% range after 60 days and then remained relatively constant. The %C content of the litter changed significantly ($p < 0.05$) over time in most sites, except in the riverine sedge fen. Also, the C content in the riverine marsh (RM) and the riverine sedge fen (RSF) decreased by approximately 5% between 365 and 456 days (Table 3.2.). None of the other peatlands exhibited this trend.

Neckles & Neill (1994) and Shure et al. (1986) found that litter decay is enhanced in sites which are inundated for at least part of the year. The RM and the RSF were the only sites which exhibited a water level above the peat surface in 1993 and I speculate that the decomposition process in the plant litter may have been advanced enough that fungi began to break down structural carbohydrates after 365 days. This would result in a marked decrease in the %C content of the litter. These same processes may not have progressed to the same degree in the other three peatlands.

Nitrogen (N) concentrations exhibited a greater change over time than carbon (C) concentrations (Table 3.2.). The intial N content ranged from 1.67% (*Carex lasiocarpa*) to 2.60% (*Typha latifolia*). The %N content of all litter types increased significantly over time ($p < 0.05$). In the LM, the %N tissue concentrations of *T. latifolia* increased by 91% over 456 days. Nelson et al. (1992) reported initial %N of *Carex* spp. litter of 2.77%, which is higher than the N concentrations found in my sedge litter. However, Bartsch & Moore (1985) and Ohlson (1987) reported results comparable to mine.

Initial C:N ratios ranged from 15.13 (*Typha latifolia*) to 22.20 (*Carex lasiocarpa*) (Table 3.3.). In the lacustrine marsh, *C. lasiocarpa* had a significantly higher C:N ratio than *T. latifolia* at most times ($p < 0.05$), except after 456 days, when the ratios were similar. This indicates that *T. latifolia* initially has higher N tissue concentrations, but over time they approach those of *C. lasiocarpa*. Furthermore, the C:N ratio of *T. latofolia* changed significantly ($p < 0.05$), whereas the C:N ratio of the sedge did not change significantly over 456 days.

In the ORF, *Carex lasiocarpa* had a significantly lower initial C:N ratio than *Salix pedicellaris*, but the ratios were similar after 60 days and remained similar for the following 396 days (Table 3.3.). The C:N ratios of *C. lasiocarpa* and *S. pedicellaris* did not change significantly over 456 days. Furthermore, the C:N ratios of *C. lasiocarpa* changed significantly in the lacustrine sedge fen (LSF), riverine sedge fen (RSF) and the riverine marsh (RM) over 456 days ($p < 0.05$). However, there was no consistent pattern of change of the C:N ratios across the sites (Table 3.3.) and the C:N ratios of *Carex* spp. litter were not significantly different at any sampling period across all sites ($p > 0.05$).

Verhoeven & Arts' (1992) results show a consistent decrease in the C:N ratio over time, but their final C:N ratio for *Carex* spp. in a Dutch fen (approximately 18) was similar to my final C:N ratios. Their results were supported by those of Szumigalski & Bayley (under review), who reported C:N ratios for *Carex* spp. in Alberta fens. Parnas (1974) developed a model which predicted that litter with a C:N ratio of 20 to 30:1 will not experience significant changes in this ratio over time. Net nitrogen mineralization rather than net immobilization will occur and equal utilization of carbon and nitrogen by decomposers will not change the C:N ratio of the plant litter significantly. The plant litter used by Verhoeven & Arts (1992) and Szumigalski & Bayley (under review) had initial C:N ratios above Parnas' (1974) critical C:N ratio, resulting in nitrogen immobilization by microbes and thus a significant decrease in the C:N ratio. My plant litter had low initial C:N ratios and changes in the ratio were generally insignificant as a result.

Decomposition of the standard litter types (*Carex aquatilis* and cellulose)

Carex aquatilis

Weight losses and rates of decomposition

The standard plant litter showed a significant difference ($p < 0.0001$) in weight losses among sites and within sites among sampling periods (30, 60, 100 days). After 100 days, *Carex aquatilis* had lost the most weight in the LM (79.8%) and the least weight (59.7%) in the RM (Figure 3.3.). Within the marshes, the weight losses ranged from 59.7 to 79.8% over 100 days. This represents a rate of decomposition of 0.0092 to 0.0161 /day (Table 3.4.). The fens exhibited weight losses ranging from 69.3 to 75.3% (rates of decomposition of 0.0117 to 0.0139 /day) over the same period (Table 3.4.). The fens and marshes, once combined into two groups, did not exhibit a significantly different rate of decomposition over 100 days in 1994 ($p > 0.05$).

Szumigalski & Bayley (under review) examined the weight losses of a standard *Carex* sp. in the ORF and a sedge fen (this study's LSF) as well, and they reported weight losses of 33% (0.0011 /day) and 31% (0.0010 /day) in these sites during the first 365 days, respectively. In contrast, the results of this study indicate weight losses of 69.9% (0.0120 /day) (ORF) and 75.3% (0.0139 /day) (LSF) over 100 days during 1994 (Figure 3.3.), approximately a ten-fold increase of the decay rate over a shorter time period. Furthermore, Szumigalski & Bayley's (under review) studies indicate first year weight losses of the same *Carex* sp. within a bog, a poor fen and a wooded moderate-rich fen of 45%, 45% (both 0.0016 /day) and 42% (0.0015 /day), respectively. These values are also lower than my findings; however, Szumigalski & Bayley's (under review) standard species was *Carex lasiocarpa* from their 'sedge fen', whereas my standard species was *Carex aquatilis* from the riverine sedge fen (RSF). Therefore, direct comparisons of these studies require caution.

Ohlson (1987) reported significant first year weight loss differences of *Carex rostrata* in a Swedish *Sphagnum* spp. dominated intermediate fen of 44% (0.0016 /day) and in a spring-area rich fen of 81% (0.0045 /day). However, Bartsch & Moore (1985) found no significant differences in weight losses of *Carex* spp. in sub-arctic poor and rich fens in Quebec (13 to 20% over the first 365 days, 0.0004 to 0.0006 /day). Based on these studies, my results are substantially higher than those of Bartsch & Moore (1985) and Ohlson (1987). I could not find any reports on decomposition studies of standard *Carex* spp. across different marshes.

C and N content and C:N ratios

The C content of the standard litter increased over 100 days but these increases were not significant ($p > 0.05$) (Table 3.5.). A similar trend was observed for local *Carex lasiocarpa* over 456 days in the same sites (Table 3.2.). The lacustrine marsh exhibited the largest increase in C content, from 45.5% to 51.3% (Table 3.5.).

The initial N content for *Carex aquatilis* was 2.15% and it decreased consistently in the fens of this study over 100 days (Table 3.5.). However, %N changes were only significant ($p < 0.05$) in the ORF and the RSF and not in the LSF. In both marshes, the %N litter tissue concentrations increased from 2.15% to 2.84% (RM) and 3.05% (LM). These increases were significant ($p < 0.05$) (Table 3.5.) and are comparable to the significant increases of %N tissue concentrations for the dominant litter types in all sites (Table 3.2.).

In the fens of this study, the C:N ratio increased consistently over time (Table 3.5.), most notably in the ORF, where it increased from 21.17 to 32.07 over 100 days. Due to the nutrient-poor status of the fens, the nitrogen source for decomposing microbes is the plant litter rather than the surrounding water. This results in the decrease of litter N concentrations and ultimately the increase of the C:N ratio over time. Conversely, the C:N ratios decreased in both marshes from 21.17 to 15.86. Decomposition in eutrophic marshes allows decomposeres to take up nitrogen from both the surrounding water as well as from the plant litter. Davis & van der Valk (1978) reported increases in litter nitrogen concentrations in *Typha glauca* and *Scirpus fluviatilis* in Goose Lake, Iowa. They attributed these increases to the microflora accociated with the plant litter, also resulting in a decreasing C:N ratio over time. Furthermore, Gallagher (1978) determined that increases in litter nitrogen concentrations can also be attributed to sorption processes and deposition of minerals in fine fissures of the plant litter. The changes in the C:N ratios were not significant in the LM and the LSF, whereas they were significant in the remaining three peatlands ($p < 0.05$).

Leaching of organic compounds from *Carex aquatilis*

Leaching of soluble organic materials from live *Carex aquatilis* tissue accounted for a weight loss of 4.66% (0.0068 /day) (with antibiotics and fungicides dissolved in 2d-H_2O) to 8.94% (0.0134 /day) (2d-H_2O only) during the first seven days *in vitro* (no significant difference, $p > 0.05$). This range is lower than findings by Ohlson (1987), who reported a mean weight loss of 14% for *Carex* *rostrata* from a Swedish mire after seven days under similar conditions. This quantity represents the amount of soluble organic compounds which leaches out of plant litter during the first phase of decomposition.

Cellulose

Weight losses and rates of decomposition

Filterpaper weight losses were significantly different ($p < 0.0001$) among sites and within sites among sampling periods (30, 60, 100 days) over 100 days in 1994 (Figure 3.3.). The weight losses ranged from 13.2 to 43.1% (0.0014 to 0.0056 /day) in the fens and from 49.7 to 84.1% (0.0069 to 0.0183 /day) in the marshes (Table 3.4.). The LM and the LSF exhibited the most and least weight losses among the five peatlands, respectively (Figure 3.3.). Generally, filterpaper lost significantly more weight in the marshes than in the fens ($p < 0.05$).

Lieffers (1988) studied cellulose degradation in peatlands and reported first year weight losses of up to 84% (0.0050 /day) in a treed fen in Alberta. In contrast, Bartsch & Moore (1985) reported cellulose weight losses of only 5% (0.0001 /day) in sub-arctic fens in Quebec over one year. Farrish & Grigal (1988) examined cellulose decomposition in a fen in Minnesota and measured a weight loss of 68% (0.0031 /day) at a depth of 5 cm below the peat surface and Laine et al. (1984) measured a 53.6% (0.0021 /day) weight loss in a Finnish mire, both over a 365 day period. The results of this study compare favourably with Laine et al.'s (1984), Farrish & Grigal's (1988) and Lieffers' (1988) findings but are considerably higher than Bartsch & Moore's (1985) values for sub-arctic fens. I could not find studies on comparative cellulose decomposition in marshes.

In comparison, cellulose lost significantly more weight in marshes (66.9%, 0.0111 /day) than in fens (28.2%, 0.0033 /day) (Figure 3.3.). Due to the eutrophic status of the marshes, decomposers were not nutrient limited which enabled them to break down the nutrient-poor filterpaper (99% cellulose). Since the fens have lower concentrations of surface water nutrients, the decomposers were inhibited from breaking down cellulose as efficiently as they did in the marshes. In contrast, the standard plant litter, *Carex aquatilis*, degraded similarily in marshes (68.8%, 0.0116 /day) and fens (72.3%, 0.0128 /day) over a 100 day period in 1994 (Figure 3.3.). The plant litter contains nutrients, carbon and energy and may have supplied the decomposing microflora with sufficient nutrients to degrade it equally effectively in fens and marshes over 100 days in 1994.

Relationship of decomposition to environmental factors

The decomposition (weight losses) of *Carex lasiocarpa* in fens over 456 days correlated best with NH_4^+ ($r = 0.73$, $p < 0.001$) and total dissolved phosphorus (TDP) ($r = 0.54$, $p < 0.01$) concentrations in the surface water (Table 3.6.). In contrast, *C. lasiocarpa* weight losses in marshes was most closely correlated with the water level elevation ($r = 0.74$, $p < 0.01$) and NH_4^+ ($r = 0.49$, $p < 0.01$) (Table 3.6.).

Furthermore, Table 3.7. shows that decomposition processes of the standard plant litter and cellulose (filterpaper) correlated best with NH_4^+ ($r = 0.89$, $p < 0.05$) and soluble reactive phosphorus (SRP) ($r = -0.70$, $p < 0.05$) concentrations in the surface waters of the fens, respectively. SRP exhibited the best correlation with weight losses of both standard litter types in marshes ($r = 0.89$, $p < 0.05$, for the standard plant litter and $r = -0.64$, $p < 0.05$, for filterpaper) (Table 3.7.).

Water level relative to the peat surface

The water level relative to the peat surface is an important factor in determining the rate of weight loss of litter in peatlands. High water levels may cause anoxic conditions, which inhibit microbe activity during decomposition (Brinson et al., 1981; Bridgham & Richardson, 1992). Results of measurements of anoxia, as determined with steel rods during the 1994 growing season, indicated that the site with the lowest water table, the riverine marsh (RM), exhibited the greatest depth of the acrotelm. Conversely, the water level in the lacustrine marsh (LM) was consistently above the peat surface and anoxic conditions prevailed within the water column. The water levels in the marshes were significantly different between years ($p < 0.05$), the RM was flooded in 1993 and dry in 1994 and the LM exhibited opposite water level regimes during both years of this study (Table 3.8.).

Decomposition of the dominant sedge proceeded at a faster rate in the LM than in the RM (a 14.2% difference after 456 days). This is possibly due to the high water level within the RM in 1993, resulting in anoxic conditions within the water column. Furthermore, the fluctuating water level in the LM may have created an environment of wetting and drying, which is believed to optimize decay processes (Brinson et al., 1981), and may have oxygenated the surface water sufficiently to allow for the rapid decay of plant litter by microbes (Malmer, 1986). The water levels in the fens were relatively stable during both years of this study and were not significant factors, which is in contrast to results from Szumigalski & Bayley (under review). They determined that the water level was the most significant parameter explaining weight losses of plant litter in fens and bogs in central Alberta in 1991 and 1992.

Surface water nutrients

Fen plant litter decomposition (weight losses) correlated best with NH_4^+, total phosphorus (TP) and TDP concentrations in the surface water (Table 3.6.). No other environmental parameters were significant. The RSF, exhibited the lowest k' (% weight loss) value (45.2) and also had the lowest concentrations of ammonium in its surface water. Both the ORF and the LSF had similar ammonium concentrations and similar weight losses of *Carex lasiocarpa* over 456 days (k' values of 64.6 and 68.5, respectively). TDP and TP also correlated significantly with weight losses of *C. lasiocarpa* in fens. However, the importance of TP must be taken with caution because there was only a weak correlation with weight loss ($r = 0.14$, $p < 0.05$). In marshes, NH_4^+ was a secondarily significant parameter correlating with decomposition of *C. lasiocarpa* but, in contrast to the fens, none of the phosphorus parameters were significant (Table 3.6.).

SRP correlated significantly with weight losses of cellulose and *Carex aquatilis* (standard plant litter) in marshes ($r = 0.64$ and -0.89, respectively, both $p < 0.05$) (Table 3.7.). It appears that NH_4^+ was the most limiting nutrient of cellulose and standard plant litter decay (k) in the three fens. SRP and pH were also significant factors (Table 3.7.). The RSF had the highest pH of the fens and also exhibited the highest cellulose weight loss over 100 days. The importance of pH in fen decomposition has to be taken with caution since none of the other acidity-alkalinity parameters, such as HCO_3^- and adjusted conductivity, exhibited significance in the analyses. These parameters are usually correlated with each other.

By combining these fens and marshes into one large group, it becomes evident that decomposition (k') of the standard plant litter correlated best with NH_4^+ ($r = 0.58$, $p < 0.05$) and TDN ($r = 0.41$, $p < 0.05$). However, it may be difficult to separate the influences of ammonium and TDN, since they were significantly correlated with each other ($p < 0.05$). The variation of cellulose decomposition correlated best with SRP ($r = 0.73$, $p < 0.01$) and TDN ($r = 0.40$, $p < 0.05$) in these fens and marshes. Thus, plant litter decomposition (weight losses) seems correlate best with NH_4^+, whereas cellulose decomposition correlated best with SRP in fens and marshes in central Alberta. Also, the plant litter may have had sufficiently high concentrations of organic phosphorus, which would supply microbes involved in the processes of decomposition with sufficient amounts of this nutrient and not limit their effectiveness.

Both NH_4^+ and TDP may be limiting to decomposers in fens, whereas the water level relative to the peat surface is primarily affecting the weight loss of indigenous plant litter in marshes. Since both marshes exhibit higher concentrations of TDP, TP and ammonium than all three fens (Table 3.8.), higher surface water nutrient concentrations seem to increase rates of decomposition in these sites. These results partially support findings by Szumigalski & Bayley (under review), who reported the significance of TDP for decay processes in peatlands in Alberta, and Widden et al. (1988), who determined that high concentrations of nitrogen in soils enhance cellulose degradation. However, Rochefort et al. (1990) found that artificial acidification of peatlands with SO_4^{2-} and NO_3^- did not increase rates of decomposition of *Sphagnum* spp. in northeastern Ontario. Also, Bayley et al. (1985) reported no increases in weight losses of wetland species in a Florida marsh after fertilization with N and P. Bridgham & Richardson (1992) also found no increases in CO_2 emissions from southern peatlands after fertilization with nutrients.

Caution has to be used when comparing different decomposition studies. Difficulties arise due to (a) different gauges and sizes of mesh bags (Brinson et al., 1981), (b) their placement within the peat horizon (Farrish & Grigal, 1988; Santelmann, 1992), (c) different environmental parameters (Nelson et al., 1992), (d) the drying temperature of the plant litter (Clymo, 1965) and (e) the degree of prior senescence of the plant litter (Ohlson, 1987).

Conclusions

Weight losses and rates of decomposition of dominant plant litter (over 456 days in 1993/94) and standard plant litter and cellulose (filterpaper) (over 100 days in 1994) have been examined in five peatlands. Differences in weight loss were partially explained by the differences in litter quality (%C, %N and C:N) and environmental parameters among these sites.

The hypothesis that the weight losses and rates of decay of the dominant and standard plant litters and cellulose increase along this fen - eutrophic marsh gradient was only partially proven. *Carex lasiocarpa*, the dominant sedge indigenous to each peatland, had losses between 45.2% (RSF) and 68.5% (LSF) in fens and between 58.1% (RM) and 72.3% (LM) in marshes over 456 days. Even though significant weight loss differences existed among individual sites, these fens and marshes, as peatland types, show no significant decay differences.

The filterpaper decayed significantly less than the standard plant litter in the fens, but both decomposed at approximately the same rate in the marshes. Leaching of soluble organic compounds accounted for a mean weight loss of 6.80% of initial dry weight in *Carex aquatilis in vitro* over seven days.

Based on this study, decomposition of plant litter in fens correlated best with NH_4^+, whereas cellulose decay exhibited a close relationship to SRP concentrations in the surface water. The water level relative to the peat surface and SRP correlated best with the weight losses of the dominant plant litter and the standard litters in marshes, respectively. In general, decomposition of *Carex aquatilis* in these peatlands was controlled by NH_4^+, whereas cellulose decay correlated significantly with SRP and TDN.

The C:N ratios of the standard plant litter increased in fens but decreased in marshes over 100 days. However, no clear trends in changes over time for this ratio were apparent for the dominant vegetation after 456 days decomposition.

Peat accumulation is believed to be the result of slow rates of decomposition rather than high rates of productivity (Clymo, 1965; Malmer, 1986; Farrish & Grigal, 1988; Vitt, 1990). Furthermore, decomposition rates in marshes are generally higher than in fens (Davis & van der Valk, 1978; Nelson et al., 1990). I did not find this trend in these boreal Alberta peatlands. It can be hypothesized that no peat, or very little, should be present in marshes and significantly more peat should be present in fens. This study contradicts that hypothesis since all of the marshes exhibited an organic soil stratum and the decomposition rates were not significantly different for the dominant vegetation in each site. Thus, fens and marshes in central Alberta may have similar peat accumulation potentials.

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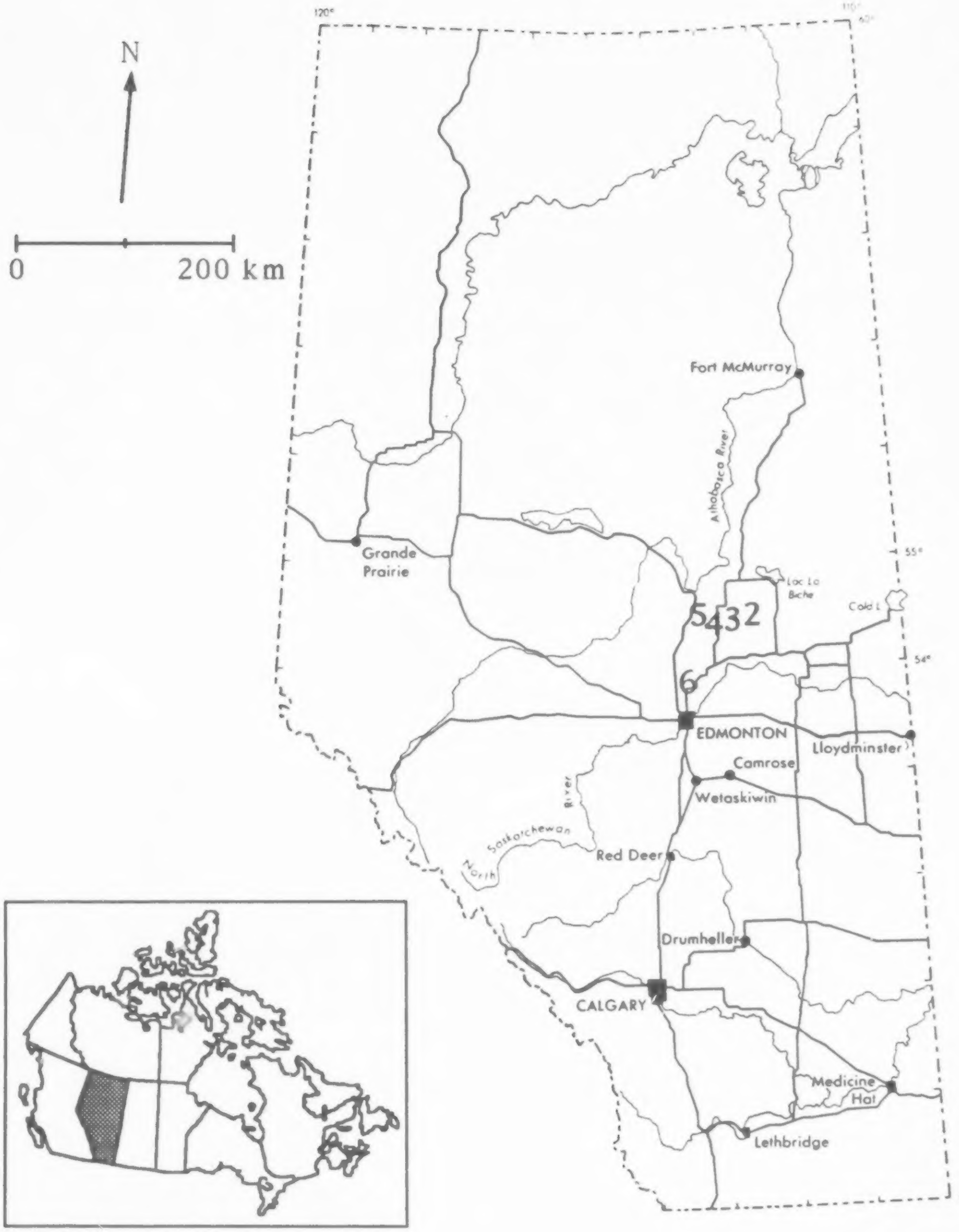
120°
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Athabasca River
Grande Prairie
Lac La Biche
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54°
6
EDMONTON
Lloydminster
Camrose
Wetaskiwin
North Saskatchewan River
Red Deer
Drumheller
CALGARY
Medicine Hat
Lethbridge
49°

Figure 3.1. Relative location of the peatlands in central Alberta (**2** = open rich fen, **3** = riverine sedge fen, **4** = lacustrine sedge fen, **5** = riverine marsh and **6** = lacustrine marsh). These sites were selected for this decomposition study from a larger group of peatlands currently under investigation.

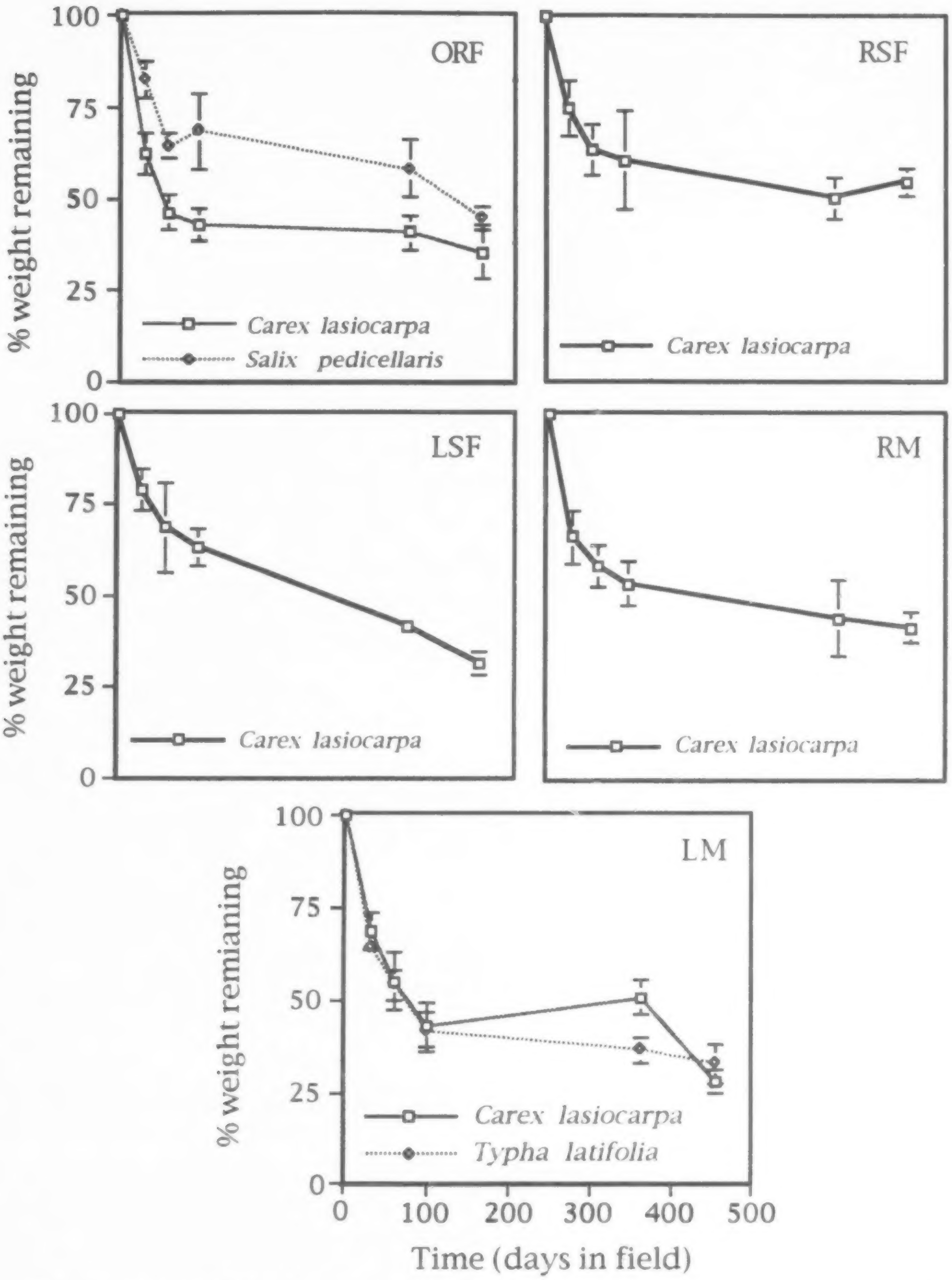

Figure 3.2. Weight losses (+/- SE) of the dominant species in five peatlands (ORF = open rich fen, RSF = riverine sedge fen, LSF = lacustrine sedge fen, RM = riverine marsh and LM = lacustrine marsh) over 30, 60, 100, 365 and 456 days in 1993/94. Error bars absent when SE < 3%.

Table 3.1. Rates of decomposition (/day) * of the dominant plant litter over 30, 60, 100, 365 and 456 days in five peatlands (ORF = open rich fen, RSF = riverine sedge fen, LSF = lacustrine sedge fen, RM = riverine marsh, LM = lacustrine marsh) in 1993 and 1994.

Site	Species	30 days	60 days	100 days	365 days	456 days
ORF	*Carex lasiocarpa*	0.0157	0.0129	0.0084	0.0024	0.0022
	Salix pedicellaris	0.0065	0.0073	0.0039	0.0014	0.0017
RSF	*Carex lasiocarpa*	0.0098	0.0076	0.0051	0.0020	0.0013
LSF	*Carex lasiocarpa*	0.0079	0.0062	0.0046	0.0024	0.0025
RM	*Carex lasiocarpa*	0.0135	0.0089	0.0062	0.0022	0.0020
LM	*Carex lasiocarpa*	0.0123	0.0100	0.0084	0.0020	0.0029
	Typha latifolia	0.0144	0.0129	0.0089	0.0027	0.0025

* simple exponential decay rate

Table 3.2. Mean (+/- SE) percent nitrogen and carbon of dominant plant litter from decomposition bags in five peatlands over 456 days in 1993 and 1994 (ORF = open rich fen, RSF = riverine sedge fen, LSF = lacustrine sedge fen, RM = riverine marsh, LM = lacustrine marsh).

Site	Species	Initial % C	30 days % C	60 days % C	100 days % C	365 days % C	456 days % C	Initial % N	30 days % N	60 days % N	100 days % N	365 days % N	456 days % N
ORF	*Carex lasiocarpa*	38.57 -- *	38.99 (1.39)	45.81 (0.46)	45.26 (0.33)	45.96 (0.82)	45.89 (0.98)	2.07 --	1.84 (0.04)	2.18 (0.10)	2.50 (0.09)	2.57 (0.21)	2.20 (0.08)
	Salix pedicellaris	36.77 --	36.97 (0.60)	41.34 (2.63)	48.87 (1.23)	46.05 (2.38)	48.36 (1.26)	1.79 --	2.25 (0.10)	2.61 (0.14)	3.15 (0.06)	2.97 (0.20)	2.84 (0.11)
RSF	*Carex lasiocarpa*	37.31 --	39.34 (0.75)	43.46 (1.01)	40.88 (2.52)	40.91 (0.88)	35.82 (3.34)	1.90 --	2.00 (0.06)	2.14 (0.11)	2.35 (0.14)	2.46 (0.12)	2.16 (0.21)
LSF	*Carex lasiocarpa*	37.54 --	36.93 (0.61)	45.00 (0.26)	44.96 (0.17)	46.75 (0.46)	45.94 (0.51)	1.85 --	1.96 (0.04)	2.49 (0.05)	2.79 (0.03)	2.66 (0.10)	2.93 (0.09)
RM	*Carex lasiocarpa*	38.08 --	42.92 (0.74)	47.71 (0.86)	45.90 (0.56)	45.56 (0.78)	40.16 (0.84)	2.09 --	1.99 (0.11)	2.57 (0.12)	2.59 (0.11)	2.51 (0.07)	2.44 (0.07)
LM	*Carex lasiocarpa*	37.10 --	39.50 (0.73)	45.01 (0.67)	44.85 (0.74)	46.65 (0.42)	47.15 (0.51)	1.67 --	2.15 (0.16)	2.54 (0.13)	2.57 (0.08)	2.58 (0.14)	3.06 (0.11)
	Typha latifolia	39.90 --	40.92 (0.89)	45.55 (1.03)	42.72 (0.97)	45.85 (0.75)	46.17 (2.64)	2.60 --	3.63 (0.28)	4.97 (0.62)	4.27 (0.32)	4.39 (0.20)	3.95 (0.80)

* = not determined

Table 3.3. Mean (+/-) C:N ratios of the dominant litter from decomposition bags in five peatlands (ORF = open rich fen, RSF = riverine sedge fen, LSF = lacustrine sedge fen, RM = riverine marsh, LM = lacustrine marsh) over 456 days in 1993 and 1994.

Site	**Species**	**Initial C:N**	**30 days C:N**	**60 days C:N**	**100 days C:N**	**365 days C:N**	**456 days C:N**
ORF	*Carex lasiocarpa*	18.63	21.20	21.23	18.21	18.63	21.00
		--*	(0.62)	(1.06)	(0.71)	(1.81)	(1.06)
	Salix pedicellaris	20.54	16.52	15.87	15.58	15.67	17.10
		--*	(0.53)	(0.72)	(0.54)	(0.80)	(0.55)
RSF	*Carex lasiocarpa*	19.64	19.79	20.46	17.43	16.81	16.65
		--*	(0.71)	(0.87)	(0.60)	(0.73)	(0.33)
LSF	*Carex lasiocarpa*	20.29	18.86	18.13	16.14	17.73	15.71
		--*	(0.31)	(0.29)	(0.17)	(0.68)	(0.40)
RM	*Carex lasiocarpa*	18.22	21.91	18.84	17.87	18.29	16.53
		--*	(1.38)	(1.08)	(0.60)	(0.76)	(0.57)
LM	*Carex lasiocarpa*	22.20	18.91	18.12	17.56	18.17	15.45
		--*	(1.53)	(1.03)	(0.78)	(1.07)	(0.45)
	Typha latifolia	15.13	11.51	9.67	10.24	10.64	12.54
		--*	(0.63)	(1.34)	(0.70)	(0.55)	(2.11)

* = not determined due to small sample size

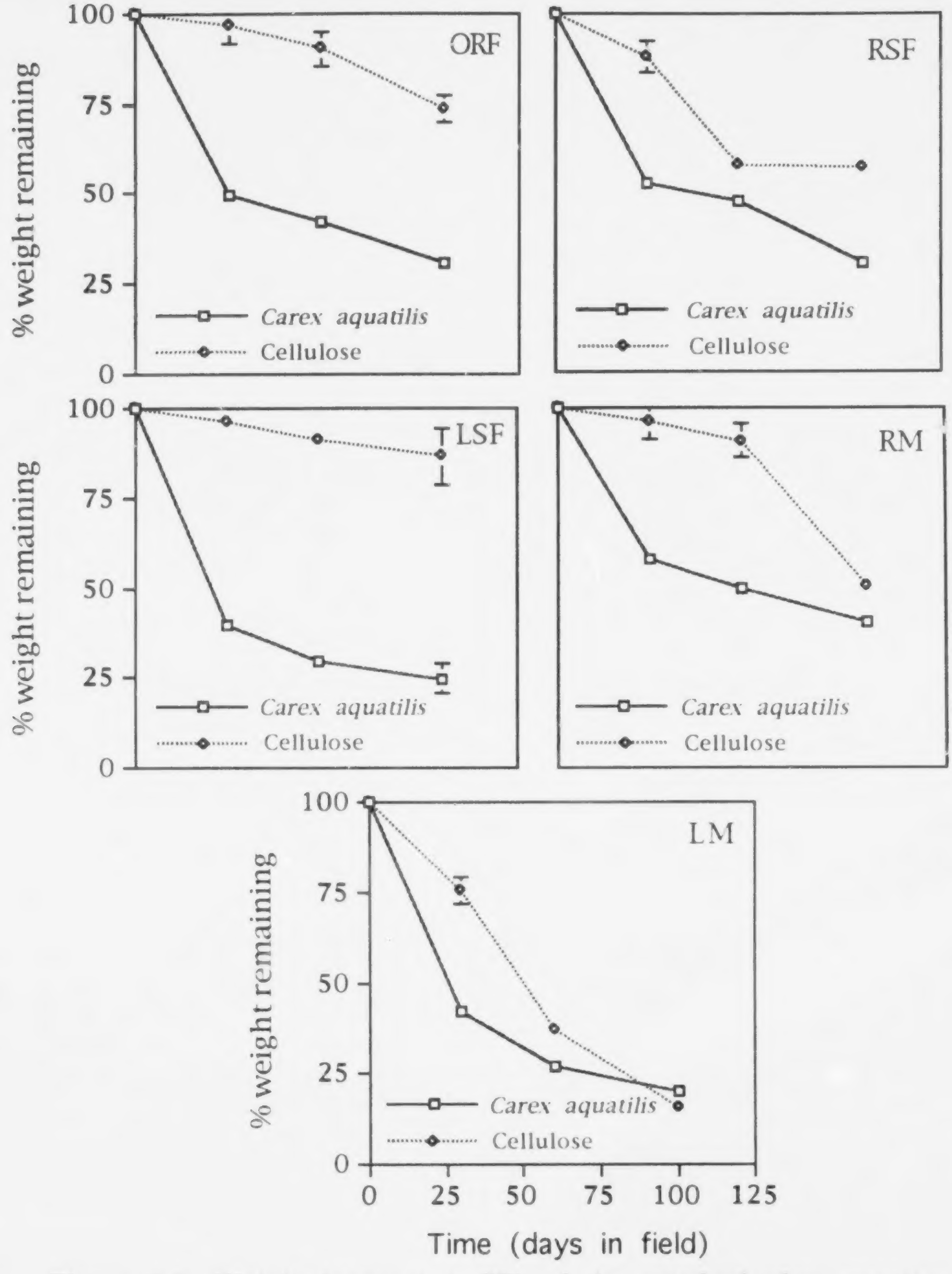

Figure 3.3. Weight losses (+/- SE) of the standard plant species and cellulose (filterpaper) in five peatlands (ORF = open rich fen, RSF = riverine sedge fen, LSF = lacustrine sedge fen, RM = riverine marsh, LM = lacustrine marsh) over 30, 60 and 100 days in 1994. Error bars absent when SE < 3%.

Table 3.4. Rates of decomposition (/day) * of standard plant litter over 30, 60 and 100 days in five peatlands (ORF = open rich fen, RSF = riverine sedge fen, LSF = lacustrine sedge fen, RM = riverine marsh, LM = lacustrine marsh) in 1994.

Site	**Species**	**30 days**	**60 days**	**100 days**
ORF	*Carex aquatilis*	0.0234	0.0145	0.0120
	Filterpaper	0.0010	0.0017	0.0030
RSF	*Carex aquatilis*	0.0214	0.0125	0.0117
	Filterpaper	0.0043	0.0093	0.0056
LSF	*Carex aquatilis*	0.0310	0.0202	0.0139
	Filterpaper	0.0011	0.0015	0.0014
RM	*Carex aquatilis*	0.0182	0.0117	0.0092
	Filterpaper	0.0012	0.0016	0.0069
LM	*Carex aquatilis*	0.0291	0.0216	0.0161
	Filterpaper	0.0093	0.0166	0.0183

* simple exponential decay rate

Table 3.5. Mean (+/- SE) percent nitrogen and carbon and C:N ratios of standard plant litter (*Carex aquatilis*) from decomposition bags in five peatlands (ORF = open-rich fen, RSF = riverine sedge fen, LSF = lacustrine sedge fen, RM = riverine marsh, LM = lacustrine marsh) over 100 days in 1994.

Site	Initial % C	30 days % C	60 days % C	100 days % C	Initial % N	30 days % N	60 days % N	100 days % N	Initial C:N	30 days C:N	60 days C:N	100 days C:N
ORF	45.50 (0.65)	46.67 (0.73)	46.15 (0.74)	47.75 (0.13)	2.15 (0.09)	1.81 (0.12)	1.69 (0.11)	1.50 (0.06)	21.17 (1.60)	26.41 (1.79)	27.98 (1.79)	32.07 (1.17)
RSF	45.50 (0.65)	44.89 (0.97)	47.85 (0.59)	44.29 (1.39)	2.15 (0.09)	1.82 (0.09)	1.82 (0.07)	1.74 (0.07)	21.17 (1.60)	24.85 (0.98)	26.39 (0.71)	25.51 (0.83)
LSF	45.50 (0.65)	47.78 (0.66)	48.49 (1.09)	49.44 (0.36)	2.15 (0.09)	1.77 (0.08)	2.05 (0.09)	2.09 (0.11)	21.17 (1.60)	27.28 (1.01)	23.85 (0.79)	23.91 (1.03)
RM	45.50 (0.65)	45.41 (0.67)	45.21 (0.77)	44.64 (1.04)	2.15 (0.09)	2.26 (0.07)	2.69 (0.10)	2.84 (0.12)	21.17 (1.60)	20.22 (0.58)	16.93 (0.71)	15.86 (0.74)
LM	45.50 (0.65)	48.82 (0.31)	50.37 (0.32)	51.32 (0.32)	2.15 (0.09)	2.42 (0.19)	2.74 (0.04)	3.05 (0.07)	21.17 (1.60)	20.71 (1.46)	18.42 (0.35)	16.87 (0.32)

Table 3.6. Correlation coefficients of weight loss (k') of *Carex lasiocarpa* with various surface water parameters and water level relative to the peat surface over 456 days in five wetlands (fens: open rich fen, lacustrine sedge fen, riverine sedge fen; marshes: riverine marsh, lacustrine marsh) in 1993/94.

	Fens		**Marshes**	
Parameter	**r**	**p**	**r**	**p**
NH4+	0.73	***	0.49	**
TP	0.14	*	n.s.	---
TDP	0.54	**	n.s.	---
Water level	n.s.	---	0.74	**

TP = total phosphorus
TDP = total dissolved phosphorus

n.s. $p > 0.05$
* $0.05 < p < 0.01$
** $0.01 < p < 0.001$
*** $0.001 < p < 0.0001$

Table 3.7. Correlation coefficients of weight losses (k') of two standard litter types with various surface water chemistry parameters over 100 days in five peatlands (fens: open rich fen, riverine sedge fen, lacustrine sedge fen; marshes: riverine marsh, lacustrine marsh) in 1994.

a.) *Carex aquatilis* from the riverine sedge fen

	Fens		Marshes	
Parameter	**r**	**p**	**r**	**p**
NH4+	0.89	*	n.s.	---
SRP	n.s.	---	0.89	*
pH	n.s.	---	n.s.	---

b.) Whatman #1 filterpaper

	Fens		Marshes	
Parameter	**r**	**p**	**r**	**p**
NH4+	0.56	*	n.s.	---
SRP	-0.70	*	-0.64	*
pH	-0.28	*	n.s.	---

SRP = soluble reactive phosphorus

n.s. $p > 0.05$
* $p < 0.05$

Table 3.8. Means (ranges) of surface water parameters in five peatlands (ORF = open rich fen, RSF = riverine sedge fen, LSF = lacustrine sedge fen, RM = riverine marsh, LM = lacustrine marsh) in 1993 and 1994.

Characteristic	**ORF**	**RSF**	**LSF**	**RM**	**LM**
pH	6.23 (5.51 - 7.37)	7.10 (6.34 - 8.06)	6.98 (6.20 - 7.77)	7.44 (6.74 - 8.37)	7.37 (6.62 - 8.08)
* Corrected conductivity (µS)	74.7 (51.0 - 86.0)	231.0 (128.0 - 342.0)	197.2 (57.0 - 286.0)	432.8 (293.0 - 717.0)	780.3 (651.0 - 1186.0)
Alkalinity (mg/L CaCO3)	27.3 (12.5 - 39.6)	99.4 (55.8 - 167.5)	75.2 (19.5 - 136.3)	201.1 (75.0 - 299.25)	242.3 (77.8 - 380.1)
HCO3- (mg/L)	33.2 (15.2 - 48.3)	121.1 (67.8 - 204.2)	91.7 (23.8 - 166.1)	243.6 (91.4 - 364.9)	295.4 (94.8 - 463.4)
NO3- (µg/L)	6.6 (1.4 - 36.0)	7.5 (1.8 - 44.2)	5.6 (0.7 - 20.7)	7.9 (2.3 - 19.7)	24.3 (2.8 - 233.2)
NH4+ (µg/L)	35.9 (1.7 - 144.7)	16.7 (1.7 - 109.9)	32.3 (0.2 - 469.9)	299.0 (2.2 - 2274.9)	431.7 (3.6 - 3515.9)
TDN (µg/L)	1184.9 (935.8 - 1781.0)	1072.2 (664.9 - 1836.6)	1027.1 (612.7 - 1594.0)	1619.6 (404.6 - 6251.0)	2648.8 (1537.0 - 5633.0)
SRP (µg/L)	8.7 (2.7 - 20.6)	20.8 (3.0 - 93.2)	4.4 (.08 - 13.6)	36.0 (2.0 - 114.3)	161.0 (8.7 - 867.1)
TDP (µg/L)	29.1 (12.7 - 42.0)	39.2 (12.7 - 99.6)	19.4 (9.3 - 46.0)	59.2 (2.9 - 116.8)	206.8 (22.7 - 1145.5)
TP (µg/L)	99.3 (34.2 - 528.8)	143.4 (17.6 - 461.4)	57.1 (13.0 - 196.9)	312.5 (97.2 - 1013.9)	433.0 (79.4 - 1864.0)
1993 Water table depth (cm)	-4.2 (-7.1 - -1.3)	7.9 (5.7 - 11)	-2.8 (-12.7 - +4.7)	32.4 (18.9 - 50.2)	-22.0 (-33.0 - -6.4)
1994 Water table depth (cm)	-3.2 (-10.1 - +4.5)	7.6 (-8.1 - +26.9)	19.6 (6.4 - 27.5)	-11.2 (-14.7 - +17.3)	22.8 (13.6 - 40.1)
* Depth of oxidation (cm)	9.8 (7.4 - 13.05)	5.4 (2.5 - 7.4)	3.9 (2.43 - 5.73)	13.5 (9.76 - 15.96)	** **

* measured only in 1994
** peat was anoxic

TDN = total dissolved nitrogen
SRP = soluble reactive phosphorus
TDP = total dissolved phosphorus
TP = total phosphorus

4. ABOVEGROUND NET PRIMARY PLANT PRODUCTION IN RELATION TO ENVIRONMENTAL FACTORS IN PEATLANDS IN BOREAL ALBERTA.

Introduction

Boreal peatlands sequester large amounts of carbon from the atmosphere via photosynthesis and release only small quantities via decomposition thereafter (Gorham, 1991; Gorham, 1988). Rates of carbon accumulation are estimated at 0.096 Pg/year (1 Pg = 10^{15} g) during the postglacial period (Gorham, 1991) and Riley (1987) and Riley & Michaud (1987) estimated that approximately 51.7% of Canada's carbon is stored in wetlands. The accumulation of carbon in wetlands is believed to be the result of slow rates of decomposition of plant matter rather than large rates of net primary production (Clymo, 1965; Farrish & Grigal, 1988; Vitt, 1990).

The effects of environmental parameters, such as water level, water chemistry and climate, on net primary production (NPP) are not clearly understood (Gorham, 1982; Reader, 1978; Richardson, 1978) and only a few studies exist, which relate these parameters to NPP. Forrest & Smith (1975) and Moore (1989) examined the relationship of water levels to NPP in peatlands and Reader (1978), Brinson et al. (1981), Backéus (1990), Grigal et al. (1985), Bartsch & Moore (1985) and Szumigalski & Bayley (under review) related water levels, surface water chemistry and some climatic parameters to NPP in peatlands. The effect of temperature on peatland NPP was previously investigated by Gorham (1974), Damman (1979) and Droste (1984). The majority of these studies concentrated on bogs and fens, whereby marshes have received less attention. The paucity of data regarding the effects of environmental parameters on marsh plant production necessitated further investigation, especially along a fen - marsh gradient during the same period.

Eriophorum vaginatum and *Carex lasiocarpa* are two common plant species in boreal North American peatlands. They are both perennial sedges which grow from belowground rhizomes each year and may produce shoots even when covered by snow and ice during the winter months (Bernard & Gorham, 1978). These "winter shoots" give them a competitive advantage over other species within the same ecosystem. Decreases in tissue nutrient levels occur each fall due to leaching and translocation of nutrients from above- to belowground tissues (Kistritz et al., 1983). Their life histories have been extensively studied (Bernard & Gorham, 1978; Auclair, 1977; Wein, 1973) and their tissue nutrient concentrations have been monitored throughout the growing season (Kistritz, 1983; Chapin III et al., 1988). Tissue nutrient concentrations of *C. lasiocarpa* have not been quantified along a fen - marsh peatland gradient in western Canada previously. The data that are available are usually restricted to either fens or marshes.

I will examine the effects of water levels, surface water nutrients and selected climatic parameters on NPP and %C, %N and TP tissue concentrations along a bog - fen - marsh gradient in central Alberta. I hypothesize that: (1) the site with the highest water level will exhibit the largest NPP due to the greatest access to the associated nutrients within the water, (2) the mean annual water level is the most dominant factor influencing the NPP of mosses, herbs and shrubs since herbs are adapted to grow in consistently high water levels and mosses and shrubs are not, (3) the nitrogen and total phosphorus tissue concentrations in *Carex lasiocarpa* in the marshes will be higher than those in *C. lasiocarpa* in the fens and *Eriophorum vaginatum* in the bog and (4) nitrogen and total phosphorus concentrations in fen and bog herbs (*C. lasiocarpa* and *E. vaginatum*, respectively) will decrease before those in *C. lasiocarpa* in the marshes. Hypotheses three and four are based on the nutrient-richer status of the eutrophic marshes when compared to the oligotrophic fens and bog.

Study area and site descriptions

The five study sites which were examined in 1993 and 1994 and an additional sixth in 1994 represent the range of peatlands present in Alberta, Canada. These included a bog, an open rich fen

(ORF), a riverine sedge fen (RSF), a lacustrine sedge fen (LSF), a riverine marsh (RM) and a lacustrine marsh (LM). The bog is located north of Bleak Lake at 54° 41' N and 113° 28' W, while the ORF (54° 28' N, 113° 17' W), LSF (54° 28' N, 113° 19' W) and the RSF (54° 28' N, 113° 18' W) are located east of Perryvale. The RM is located northwest of Perryvale at 54° 28'N and 113° 23' W, and the LM is located northeast of Clyde (54° 10' N, 113° 34' W) (Figure 4.1.).

Mild summers and cold, snowy winters characterize the climate of central Alberta (Vitt et al., in press). The long term mean annual temperature is 1.7 °C (Environment Canada, 1982), and the total mean precipitation is approximately 500 mm for all sites. Appendix 1 summarizes the climatic data for the 1993 and 1994 growing periods for all sites. All six peatlands lie within the Boreal Forest Region of Canada (Rowe, 1972). Vascular plant nomenclature follows Packer (1983), whereas "brown" moss nomenclature follows Anderson et al. (1990) and *Sphagnum* nomenclature is in accordance with Anderson (1990). Hepatics nomenclature corresponds with Vitt et al. (1988).

General descriptions of the sites are as follows:

Bog

The bog is a large, raised ombrotrophic island within a large peatland complex. The peat surface is raised about 0.3-0.5 m above an adjacent poor fen water track. The peat is 5 m thick and is arranged in large, dry hummocks, which are separated by intermittent wetter hollows. The pH of the open water in the hollows ranged from 3.7 to 4.1. A sparse tree layer of *Picea mariana* (Mill.) BSP. covers about 25% of the wooded part of this bog. *Ledum groenlandicum* Oeder dominates the ericaceous shrub layer (covers about 75%) while the sparse herb stratum consists primarily of *Smilacina trifolia* (L.) Desf.. *Sphagnum fuscum* (Schimp.) Klinggr. comprises about 90% of the moss layer with intermittent *S. angustifolium* (C. Jens. *ex* Russ.) C. Jens. and *S. magellanicum* Brid. on mid-hummocks and *Polytrichum strictum* Brid. on dry hummocks. Szumigalski & Bayley (under review) studied this site in 1991 and 1992.

Lacustrine Sedge Fen

This site is a large expanse of sedge dominated peatland situated aside a large body of water (approximately 62 ha) in a former north-south drainage channel (Vitt et al., in press) with 2-2.5 m of peat. The topography of this fen is mainly flat with the occasional small hummock (about 5% of the peatland surface). The lacustrine sedge fen was largely inundated with water for most of 1991, characteristic of a marsh, but began to dry out in 1992; therefore, Vitt et al. (in press) classified this peatland as an extreme-rich fen. In 1993, this site continued to dry out but in 1994 it was once again flooded, possibly due to beaver dams blocking outflows of the former drainage channel. The pH of the surface water ranged from 6.1 to 6.9. The vascular vegetation consists primarily of *Carex lasiocarpa* Ehrh.. Shrubs comprise only about 5% of the peatland cover and consist of *Salix pedicellaris* Pursh and *Betula pumila* L. *var. glandulifera* Regel exclusively. The moss stratum is discontinuous and dominated by *Drepanocladus aduncus* (Hedw.) Warnst. in wet pools and by *Aulacomnium palustre* (Hedw.) Schwaegr. on top of dry hummocks. Szumigalski & Bayley (under review), who studied this site in 1991 and 1992, referred to this fen as a 'sedge fen'.

Riverine Sedge Fen

This peatland is part of an extensive wetland complex adjacent to the aforementioned lacustrine sedge fen and has an approximate peat depth of 1 m. The pH of the surface water ranged from 6.3 to 8.1 during 1993 and 1994. It receives water from a discrete inflow at the southern end and the outflow at the northern end controls the water level elevation. The water level was above the peat surface during the 1993 and 1994 growing seasons. In the spring of 1994, a constructed dam blocked the outflow and, as a result, the water level was substantially higher during the second growing season. The vascular vegetation stratum is dominated by *Carex aquatilis* Wahlenb., mosses are very sparsely distributed and shrubs are absent. Also, the thalloid liverwort *Marchantia polymorpha* L. was present.

Open Rich Fen

This fen is a floating mat surrounding a small body of water. The peat surface is a uniform carpet which fluctuates with the water table of the associated slough. The peat is approximately 1 m thick floating over 1-1.5 m of water below which an additional 1-1.5 m of peat are located. The vascular plant stratum is dominated by *Carex lasiocarpa* Ehrh. and in addition to four other species of *Carex* cover about 90% of the surface. Other herbs present are *Triglochin maritima* L., *Potentilla palustris* (L.) Scop. and the insectivorous, perennial herb *Drosera rotundifolia* L.. The shrub layer consists predominantly of *Salix pedicellaris* Pursh, *Andromeda polifolia* L. and *Oxycoccus quadripetalus* Gilib., whereas the moss stratum is dominated by *Sphagnum warnstorfii* Russ. and *Aulacomnium palustre* (Hedw.) Schwaegr.. The latter two species comprise about 80% of the moss cover in this fen. In comparison to the other five sites, the open rich fen had the highest species diversity. The pH of the surface water ranged from 5.5 to 7.4 during the 1993 and 1994 growing seasons.

Riverine Marsh

This site is located on the floodplain of Tawatinaw River. During 1993, this marsh was periodically inundated with water and the water table was consistently above the peat surface. In 1994, a beaver dam just above the study area retained much of the stream flow and the water table dropped well below the peat surface. The pH of the surface water ranged from 7.1 to 8.4, and the peat is less than 1 m deep. The vascular vegetation layer is dominated by *Carex aquatilis* Wahlenb. during spring and early summer, but *Calamagrostis canadensis* (Michx.) Beauv. and *C. inexpansa* A. Gray were dominant during late summer and early fall. During their period of vegetation domination, these species cover about 95% of the surface. A number of other herb species are sparsely distributed. There are no moss and shrub strata present.

Lacustrine Marsh

This marsh is situated on the northwestern shore of Wakomao Lake (approximately 360 ha). Water flows into this lake from a drainage basin to the north (approximately 7800 ha) and from an artesian well area along the southwestern shore (approximately 300 ha). Water leaves through a small creek at the southern tip of Wakomao Lake. During 1993, the water table was below the peat surface but in 1994, this site was flooded with water, possibly due to beaver dams or man made dams blocking the outflow(s) of Wakomao Lake. The lake receives secondarily treated wastewater from Clyde (population < 1000) each spring and additional nutrients from agricultural run-off. No moss stratum exists and the vascular vegetation layer is dominated by *Carex aquatilis* Wahlenb. and *Typha latifolia* L.. Together these two species cover approximately 80% of the surface. The peat depth is 1.5-1.75 m and the pH of the surface water ranged from 7.1 to 8.1.

Methods

Production measurements

A detailed outline of the methods employed to measure the net primary production of the moss, herb, shrub and tree strata is in Chapter two.

Moss growth was measured in the bog and the open rich fen (ORF) from May until mid-October in 1993 and 1994 via the cranked wire method (Clymo, 1970). In the lacustrine sedge fen, moss production was determined by harvesting the moss mat in quadrats and then determining each year's growth by innate characteristics.

Multiple harvests were used to measure herb and shrub production within all sites. Randomly placed 0.25 m^2 quadrats were used to collect all vascular vegetation within 250 m^2 plots located adjacent to those used to determine moss production. Due to the smaller size of the ORF, these plots were only 125 m^2 large. Harvests were performed in late June, late July and late August in 1993 and

1994. Tree production was estimated from Szumigalski & Bayley (under review).

Water chemistry

Water samples were collected bimonthly from May until the end of October each year. These samples were taken from the same location within each site, a depression dug into the peat surface. The conductivity of each sample was measured in the lab within 24 hours of collection and later corrected for pH and temperature (Sjörs, 1950).

All water samples were filtered initially with GFC filters. Base cations (Na^+, Ca^{2+}, Mg^{2+}, K^+) were fixed with 0.5 mL concentrated HNO_3 and then analyzed with a Perkin-Elmer Atomic Absorption Spectrometer. Nitrate (NO_3^-), soluble reactive phosphorus (SRP) and total dissolved phosphorus (TDP) samples were re-filtered with a 0.45 µm millipore filter. Nitrate and ammonium (NH_4^+) samples were analyzed on a Technicon Auto Analyser II within 24 hours of collection. Total phosphorus (TP), SRP and TDP analyses followed Bierhuizen & Prepas (1985). Alkalinity was determined via the electrometric titration technique employing the phenolphthalein technique developed by Environment Canada (1979). Vitt et al. (in press) used the same methods.

Water levels

Water level fluctuations were measured with Steven's F water level recorders within each site except the bog, where a permanently attached meter stick was used to monitor water level changes over time. The latter method was also applied in the other five sites to supplement the water level recorder measurements. A pore water sampler was used to determine the annual position of the water level relative to the peat surface. These measurements were then related to those of the Steven's F water level recorders and meter sticks.

Depth of oxidation

A total of 15 steel welding rods (1.0 m long) were placed in each site in early May, 1994. These were inserted to a depth of 0.8 m into the peat and three replicates were removed at monthly intervals until October. The distance from the peat surface to the lowest extent of rust on each rod was measured and assumed to be the depth of the acrotelm. The mean of all measurements from June until October inclusively determined the depth of the acrotelm within each site. The methods for this technique follows those outlined by Bridgham et al. (1991).

%C, %N and TP analyses

Carbon (C) and nitrogen (N) were analyzed as described by Szumigalski & Bayley (under review). Total phosphorus (TP) was analyzed with the molybdophosphovanadate method with an Auto Analyzer as outlined by Parkinson & Allen (1975) and Prepas & Rigler (1982). Plant samples originated from quadrats clipped as part of the production study in late June, late July and late August within each site.

Eriophorum vaginatum from the bog and *Carex lasiocarpa* from the remaining three fens and two marshes were selected for analyses of C, N, and TP tissue concentrations. Four randomly selected samples from each site from late June, late July and late August in 1993 and 1994 were ground and analyzed for C and N content in a Model 440 Elementary Analyzer (Control Equipment Corp.). The nutrients were expressed as %C and %N of total dry weight and the C:N ratio was determined by dividing %C by %N for each sample. TP was expressed as µg/g of dry weight or as %TP.

Statistical analyses

Linear simple regressions between the water level relative to the peat surface and peak herb and terminal shrub production (square-root and natural-log transformed, respectively) values were performed for 1993 (n=4 sites, n=10 samples/site) and 1994 (n=5 sites, n=10 samples/site). Pearson correlation coefficients were determined to indicate the relationship between these two parameters.

ANOVAs were employed to examine changes of the C:N ratio and total phosphorus (TP) tissue concentrations of the dominant vegetation over time within and among sites (n=6 sites, n=4 samples/site/sampling period/year). Tukey tests were performed to make pairwise comparisons between %C, %N, C:N and TP within and among sites over time.

Multiple stepwise regressions (forward) were used to examine the relationship among surface water nutrients (n=13 samples/nutrient/year) and vascular and total plant net primary production in fens (n=3) and marshes (n=2), individually and combined (n=5). The bog was not included in these analyses as it was sampled only in 1994 and did not have sufficient data points for a regression.

Autocorrelation analyses were performed for each surface water nutrient within each site in order to establish any correlation between successive samples. Pearson correlation coefficients were determined between all surface water nutrients within each site to establish if any of these nutrients were correlated with each other.

Most statistical analyses were performed on SAS (SAS Institute Inc., 1989) except for the simple linear regressions, which were performed on Quattro Pro (Borland International Inc., 1992), and the autocorrelation analyses, which were executed on SYSTAT (SYSTAT Inc., 1992).

Results and discussion

Surface water chemistry and water level characteristics of the six peatlands

The lacustrine sedge fen (LSF) had the lowest surface water concentrations of NO_3^-, total dissolved nitrogen (TDN), soluble reactive phosphorus (SRP), total dissolved phosphorus (TDP), total phosphorus (TP) and Mg^{2+} (Table 4.1.). The lacustrine marsh (LM) exhibited the highest nutrient concentrations of NO_3^-, NH_4^+, TDN, SRP, TDP, TP, Na^+ and Ca^{2+}. The remaining peatlands exhibited surface water nutrient levels intermediate to those found in the LSF and LM.

The pH ranged from 3.89 (bog) to means of 6.77 for the fens and 7.41 for the marshes, and adjusted conductivity, alkalinity and HCO_3^- surface water concentrations increased along the bog - fen - marsh gradient in 1993 and 1994 (Table 4.1.).

Concentrations of base cations increased along the peatland gradient. Sodium (Na^+) and Ca^{2+} surface water concentrations were significantly higher in the marshes than in the fens and the bog ($p < 0.05$), whereas Mg^{2+} concentrations were similar in all sites (Table 4.1.).

NO_3^- did not vary significantly ($p > 0.05$) among the sites, except for the LM, where surface water concentrations were significantly higher ($p < 0.05$) (Table 4.1.). NH_4^+ was similar in the bog and the three fens but it was significantly lower than in the marshes. Surface water concentrations ranged from means of 28.6 µg/L to 365.4 µg/L in the fens and marshes, respectively. TDN exhibited trends similar to NH_4^+. Significantly lower ($p < 0.05$) surface water concentrations of TDN prevailed in the bog and the three fens (mean of 1,117.4 µg/L) compared to the marshes (mean of 2,134.2 µg/L).

SRP concentrations were similar in most sites (mean of 18.0 µg/L), except for the LM, which exhibited a mean concentration of 161.0 µg/L (significant at $p < 0.05$) during both growing seasons (Table 4.1.). The LSF had the lowest concentrations of SRP (mean of 4.4 µg/L). TDP exhibited trends similar to SRP (Table 4.1.). The bog and the fens had similar surface water concentrations of TP but they were significantly lower than those found in the marshes. Mean values ranged from 102.5 µg/L, in the bog and the three fens, to 372.8 µg/L, in both marshes, a 3.5-fold increase.

Significant water level differences between 1993 and 1994 were detected in the LSF, the riverine marsh (RM) and the LM ($p < 0.01$) (Table 4.1.). In the LSF and the RM, the water levels were below the peat surface in 1993 but above the peat surface in 1994. The LM exhibited a converse trend. No significant water level differences between years were observed in the open rich fen (ORF) and the riverine sedge fen (RSF). A lower water level was correlated with the depth of the acrotelm (measured as depth of oxidation in 1994) (Table 4.1.). The bog had the lowest water level relative to the peat surface during the 1993 and 1994 growing seasons (mean of -42.1 cm) and the depth of oxidation was greatest in this site (27.5 cm). The LM had a mean water level above the peat surface (22.8 cm in 1994) and the peat was completely anoxic (as determined by the rust-free steel rod below the peat surface).

Non-vascular plant (moss) net primary production in relation to environmental characteristics

Moss production was more variable between years than among sites within each year. The open rich fen (ORF) and the lacustrine sedge fen (LSF) exhibited 5.5-fold and 4.5-fold increases in moss NPP from 1993 to 1994, respectively. Mean moss production in the bog was greater than in the fens (211.9 g/m^2/year versus 121.8 g/m^2/year).

Although the effects of surface water nutrients on moss production were not directly tested (the sample size was too small for a regression), surface water nutrient concentrations were monitored on a bimonthly basis.

Bog

Sphagnum fuscum NPP increased from 155.9 g/m^2/year, in 1993, to 261.8 g/m^2/year, in 1994, and during this time, the mean annual water level relative to the peat surface dropped 4.9 cm. A similar trend was observed by Vitt (1990) in bogs in Ontario, where *S. fuscum* production increased over a three year period, despite an increase in drought (from 69 g/m^2/year to 119 g/m^2/year). However, the results of this study and Vitt's (1990) contradict those of Wieder & Lang (1983) and Backéus (1988). They reported a decrease in *Sphagnum* spp. NPP in response to a lower water level. Furthermore, Vasander (1982) and Hillman et al. (1990) found that *Sphagnum* spp. and "brown" mosses showed decreased growth and vigor in drained peatlands.

Backéus (1988) reported a correlation between the timing and quantity of precipitation and *Sphagnum* spp. growth during the month of June. My results support his findings. Although there were more days with precipitation in June 1993 than in June 1994 (12 days versus 9 days in 1994, respectively), the total precipitation was greater in June 1994 (90.2 mm versus 73.4 mm in 1993). Also, Brock & Bregman (1989) and Moore (1989) found a positive correlation between air temperature and *Sphagnum* spp. growth. The mean temperature from May to October was 1 °C higher in 1994 (12.4 °C) and the number of growing degree days (GDD) was greater in 1994 (1415.9 versus 1349.7 in 1993). Therefore, temperatures may have been more favorable for the growth of *Sphagnum fuscum* in the second year of this study.

Several studies showed that moss growth may be limited by nutrients, particularly nitrogen and phosphorus (Brock & Bregman, 1989; Malmer, 1990; Vitt, 1990; Aerts et al., 1992). Higher concentrations of NH_4^+, SRP, TDP and TP were detected in the surface water during the second year of this study, possibly explaining the large increase in moss NPP ($p < 0.05$). All other surface water nutrient concentrations were similar in 1993 and 1994. It is unclear whether the lowered water level or the higher nutrient concentrations contributed to the increase in moss growth.

Open rich fen

In the open rich fen (ORF), moss NPP increased 5.5-fold from 1993 to 1994 (from 51.2 g/m^2/year to 287.4 g/m^2/year). The two moss species monitored were *Sphagnum warnstorfii* and *Aulacomnium palustre*, two widespread species in peatlands in western Canada (Gignac et al., 1991). *Sphagnum warnstorfii* NPP increased from 24.8 g/m^2/year to 206.4 g/m^2/year, whereas *A. palustre* NPP increased from 27.2 g/m^2/year to 80.9 g/m^2/year.

The increase in NPP was greater for *Sphagnum warnstorfii* (8.3-fold) than for *Aulacomnium palustre* (2.8-fold), supporting findings by Gignac et al. (1991). They determined that *S. warnstorfii* is more responsive to changes in water level elevation than *A. palustre* within continental moderate-rich fens. Even though the water level rose by only 1 cm from 1993 to 1994, I speculate that this increase was sufficient to cause the significant increase in moss production, especially that of *S. warnstorffii*. None of the surface water nutrient concentrations were significantly different from the first to the second year (Table 4.1.).

Timing and quantity of precipitation (Backéus, 1988), air temperature (Brock & Bregman, 1989; Moore, 1989) and the larger number of GDD were also influencial in increasing moss growth during the second year of this study.

Lacustrine sedge fen

NPP of *Drepanocladus aduncus* increased from 26.8 g/m^2/year in 1993 to 120.8 g/m^2/year in 1994. Szumigalski & Bayley (under review) examined this species' growth and found that its NPP decreased from 1991 to 1992. They also reported of a decreasing water level relative to the peat surface. *Drepanocladus aduncus*, a submerged, hollow species, experiences a maximum growth rate at a water depth of approximately 15 cm (Gignac et al., 1991). If the water level drops below the peat surface, this species will experience stress and reduced growth rates, as supported by Szumigalski & Bayley (under review) between 1991 and 1992, and 1993 (this study). In 1994, the water level rose above the peat surface (19.6 cm) (Figures 4.2. & 4.3.) and *D. aduncus* NPP increased again.

In addition, the larger number of GDD and higher mean May to October temperature in 1994 may also be responsible for the increased moss NPP within this site during the second year of this study. Mean surface water nutrient concentrations were not significantly different between 1993 and 1994 ($p > 0.05$).

Mosses were very sparsely distributed in the riverine sedge fen and their NPP was not determined. A moss stratum was absent in the riverine and lacustrine marshes in 1993 and 1994 (Figure 4.4.).

Vascular plant net primary production in relation to water levels, surface water chemistry parameters and climatic parameters

Vascular plant production ranged from 178.1 g/m^2/year in the bog to means of 266.2 g/m^2/year in the three fens and 539.9 g/m^2/year in the two marshes during 1993 and 1994. The lacustrine marsh (LM) exhibited the highest (757.3 g/m^2/year) and the bog the lowest (178.1 g/m^2/year) vascular plant NPP. Vascular plant production correlated best with SRP ($r = 0.80$, 1993) and TP ($r = 0.67$, 1994) in the fens (Table 4.2.).

Total plant production ranged from 389.9 g/m^2/year in the bog to means of 347.3 g/m^2/year in the three fens and 539.9 g/m^2/year in the two marshes during both years of this study. The highest (757.3 g/m^2/year) and lowest (276.9 g/m^2/year) mean total NPP were present in the lacustrine marsh (LM) and in the lacustrine sedge fen (LSF) (Figure 4.4.).

Surface water concentrations of NO_3^- ($r = 0.85$, 1993) and TP ($r = 0.74$, 1994) correlated best with the total plant net primary production within the three fens (Table 4.2.). Marsh vascular and total plant NPP correlated best with alkalinity ($r = 0.87$, 1993) and SRP ($r = 0.92$, 1994) (Table 4.2.). None of the base cations concentrations correlated significantly with either vascular or total plant production in these peatlands in 1993 or 1994 ($p > 0.05$).

Both vascular and total production in all six peatlands correlated best with adjusted conductivity ($r = 0.80$, $r = 0.78$) and SRP ($r = 0.76$, $r = 0.69$) during 1993 and 1994 (Table 4.3.). NO_3^- was also correlated significantly with vascular and total plant NPP in 1993 ($r = 0.53$, $r = 0.48$, respectively).

Herbs

Herb production increased significantly along the bog - fen - marsh peatland gradient ($p < 0.01$) (Figure 4.4.). Also, herb NPP varied significantly between years within most sites (except the bog, which was measured only in 1994) ($p < 0.05$). The bog exhibited the lowest herb NPP of all the sites (34.5 $g/m^2/year$). The fens and marshes averaged an herb NPP of 249.0 $g/m^2/year$ and 539.9 $g/m^2/year$ during 1993 and 1994, respectively.

Water level relative to the peat surface

Szumigalski & Bayley (under review) reported that herb production is closely correlated with water levels in Alberta peatlands ($r = 0.88$ in 1991 and $r = 0.83$ in 1992). Laitinen (1990) showed that herbs, specifically *Carex* spp., are more tolerant of water saturated soils than shrubs. The results of this study support both of their findings. Herb NPP was correlated with water levels ($r = 0.65$ in 1993, $r = 0.80$ in 1994) (Figure 4.5.), although the correlation was weaker than that of Szumigalski & Bayley (under review).

The mean growing season water level dropped by 43.6 cm from the first to the second year in the riverine marsh (RM) and peak herb production decreased by 25%. Conversely, in the lacustrine marsh (LM), the mean growing season water level rose by 44.8 cm from 1993 to 1994 and herb production increased by 60%. However, the most prominent herb production increase occurred in the lacustrine sedge fen (LSF). The mean growing season water level rose by 22.4 cm from 1993 to 1994 and herb production increased by 376%. Szumigalski & Bayley (under review) reported that a drop of 14 cm in the water level caused the herb NPP to decrease by 40% in the same site between 1991 and 1992. It appears that the nutrients associated with the water column played a more prominant role affecting herb NPP in the nutrient-poorer LSF than they did in the nutrient-richer LM. This is evident from the comparably "small" mean water level change in the LSF between 1993 and 1994, which resulted in the most significant increase in herb NPP.

Vasander (1982) and Hillman et al. (1990) reported that drainage of peatlands reduced herb growth in a Finnish bog and a bog in northern Alberta, respectively. Furthermore, Lieffers & Shay (1982) examined the net primary production of sedges in saline prairie marshes and also reported a close relationship between the water level and NPP. *Typha* spp. and *Scirpus* spp. dominated marshes are generally more productive than *Carex* spp. dominated peatlands since the former tend to be dominant in wetlands with a higher water level (Richardson, 1978). Bayley et al. (1985) also reported that increasing water levels result in increased herb production in a Florida marsh. Bray (1963) examined a Minnesota marsh, where the water level fluctuated significantly throughout the growing season, and reported an herb production value of 1,360 $g/m^2/year$. Conversely, Boyd (1971) reported herb NPP values ranging from 530 $g/m^2/year$ to 1,132 $g/m^2/year$ in a marsh in South Carolina. However, the water level in this marsh did not fluctuate significantly throughout the growing season. This suggests that the flow rate of water may be more important than surface water nutrient concentrations in marshes (Gorham, 1974).

Climatic variables

Temperature and growing degree days (GDD) are directly linked. Gorham (1974) related the growth of two *Carex* spp. to summer temperature and Droste (1984) related *Carex* spp. production to GDD. The mean growing season temperature and the number of GDD were higher in 1994 than in 1993 (Appendix 1) as was the herb production in most sites, except in the riverine marsh. This provides further support for the prominent role of water level fluctuations, rather than climate, in affecting herb production.

Surface water nutrient concentrations

Vermeer & Verhoeven (1987) found no correlation between nutrients (N, P, K) in surface waters and herb biomass in mesotrophic fens in the Netherlands. However, they hypothesized that P may be limiting herb production in their fens. Szumigalski & Bayley (under review) determined that herb production was more closely related to water levels than to either P or N.

Ombrotrophic ecosystems are thought to be nutrient-poor and, therefore, unproductive systems (Vasander, 1982; Backéus, 1990). However, my results show that the bog in this study is just as, or more, productive than the fens during 1993 and 1994. Total production of the bog was higher than that of the LSF and the ORF (389.9 $g/m^2/year$ versus 276.9 $g/m^2/year$ and 355.8 $g/m^2/year$, respectively). These results are supported by those of Szumigalski & Bayley (under review), who determined their bog to be also equally, or more, productive than some of their fens in Alberta in 1991 and 1992. Furthermore, Francez (1992) reported similar findings which he interpreted to be the result of a more efficient nitrogen re-cycling mechanism in bogs.

The bog had higher surface water concentrations of NO_3^-, TDN, SRP, TDP and TP than the LSF, and the latter three nutrients were also higher than those in the ORF (although these differences were not significant in all cases) (Table 4.1.).

Drosera rotundifolia L. and *Utricularia intermedia* Hayne, both insectivorous species, flourish in the ORF and LSF, respectively. Dickinson (1983) determined that insectivorous and carnivorous plants are often found in nutrient-poor ecosystems. Furthermore, Wassen & Barendregt (1992) reported that *Carex lasiocarpa* is characteristically found in peatlands with low surface water nutrient concentrations. My findings are similar; both the ORF and the LSF are dominated by this sedge and have the lowest surface water concentrations of NO_3^-, SRP and TDP.

Shrubs

Shrub production decreased significantly along the bog - fen - marsh gradient ($p < 0.05$) but NPP of this stratum did not vary significantly between years in the ORF and LSF ($p > 0.05$). In the bog, shrubs contributed 126.2 $g/m^2/year$, or 32.4%, to the total production (measured only in 1994), whereas the fens averaged 27.7 g/m^2/year, or 8.0%.

Water level relative to the peat surface

Terminal shrub production was negatively correlated with water levels ($r = -0.76$ in 1993, $r = -0.72$ in 1994) (Figure 4.6.). Szumigalski & Bayley (under review) reported a similar relationship between these two variables in Alberta peatlands ($r = -0.72$ in 1991, $r = -0.70$ in 1992).

The bog had the lowest water level relative to the peat surface and exhibited the highest shrub production of those sites with a shrub stratum. Vasander (1982) and Hillman et al. (1990) reported an increase in shrub production after draining peatlands in Finland and northern Alberta, respectively. Vasander (1982) showed that dwarf shrubs show a greater response to lower water levels than tall shrubs. Hillman et al. (1990) stated that deciduous shrubs show an increase in growth and that ericaceous shrubs show either less growth and vigor or no changes at all due to a lower water level. My results support those of Hillman et al. (1990). The bog had the lowest water level and the greatest deciduous shrub production (36.3 g/m^2/year in 1994). The open rich fen (ORF) averaged 15.3 g/m^2/year in 1993 and 13.1 g/m^2/year in 1994 and the lacustrine sedge fen (LSF) averaged 14.2 g/m^2/year (1993) and 13.8 g/m^2/year (1994) of deciduous shrub production. Even though these mean NPP values are not significantly different in the latter two sites, deciduous shrub production tended to decrease with higher water levels.

It has been demonstrated that shrub production is greater on hummocks than in hollows (Backéus, 1990; Wallén et al., 1988; Moore, 1989), as waterlogged soils inhibit oxygen absorption by shrub roots (Reader, 1978). The results of this study support those of Backéus (1990), Wallén et al. (1988) and Moore (1989) as shrubs grew almost exclusively on dry hummocks rather than in wet hollows in the LSF. Also, the bog with the lowest water level exhibited the highest shrub production.

A shrub stratum was not present in the riverine sedge fen (RSF) and either marsh, possibly a result of the consistently high water level, which may inhibit seed germination. Kozlowski et al. (1991) showed that a raised water level decreases oxygen transfer to seedlings and roots of woody plants. This may reduce vegetative and reproductive growth and may lead to death.

Climatic variables

Since total shrub production did not vary significantly between years (ORF and LSF). It appears that established shrubs were not greatly affected by the mean annual temperature, amount of growing season precipitation or GDD in these peatlands in 1993 and 1994.

Surface water nutrient concentrations

Few studies relate shrub production to surface water nutrients. Reader (1982) reported an increase in ericaceous shrub growth with increased conductivity in southern Manitoba peatlands. Szumigalski & Bayley (under review) contrast these findings and report a close relationship between P and shrub growth in Alberta peatlands. Vasander (1982) supports their results and determined that shrub NPP increased after fertilization with N, P and K in fens in the Netherlands.

Trees

A significant tree cover was present only in the bog and it contributed only 7% to the total production within this site (Figure 4.4.). Szumigalski & Bayley (under review) estimated *Picea mariana* production from five year increments to be approximately 27 $g/m^2/year$.

Hillman et al. (1990) showed that tree growth is enhanced in aerated and dry peatland soils in northern Alberta. Supportingly, Jeglum (1974) demonstrated that tree growth is inhibited in wet, waterlogged soils in northern Ontario. The bog had the lowest water level relative to the peat surface (mean of -42 cm) and the greatest depth of oxidation (27.5 cm in 1994). All other sites were characterized by higher water levels and shallower depths of oxidation (Table 4.1.).

Vascular and total plant production of all six peatlands in relation to environmental parameters

The variation in both vascular and total plant production in all six peatlands correlated best with adjusted conductivity ($r = 0.80$, $r = 0.78$) and SRP ($r = 0.76$, $r = 0.69$) surface water concentrations during 1993 and 1994 (Table 4.3.).

Szumigalski & Bayley (under review) did not include NO_3^- in their analyses as NO_3^- surface water concentrations were similar in their sites. In this study, NO_3^- may be a limiting factor for plant production in the bog and fens but not necessarily in the eutrophic marshes since NO_3^- concentrations were significantly higher in the marshes.

Szumigalski & Bayley (under review) reported a strong positive and negative correlations between adjusted conductivity and herb and shrub production in Alberta bogs and fens, respectively. I did not separate these two vegetation strata but combined them as a "vascular vegetation" group; however, adjusted conductivity proved to be an important parameter explaining the variation of total production in fens and marshes in Alberta in both 1993 and 1994.

SRP related best to vascular and total plant production in 1994 and may be an important factor in controlling plant production in Alberta peatlands (Table 4.3.). Similarily, Szumigalski & Bayley (under review) reported a significant positive correlation between SRP and shrub production in Alberta peatlands in 1991 and 1992.

Rates of water flow, water level fluctuations, rates of nutrient mineralization and succession within each site may all influence vegetation production and mask the effects of chemical factors. Gorham (1950) determined that competition between vegetation strata also decreases the effects of surface water nutrients on plant growth in peatlands.

Carbon, nitrogen and phosphorus content of tissues from the dominant vegetation

The carbon content of *Carex lasiocarpa* and *Eriophorum vaginatum* in June ranged from 43.48% to 44.94% in 1993 and from 43.85% to 45.30% in 1994 (Table 4.4.). There were no significant differences in the carbon content of the plant tissues among sites, years or species nor within sites throughout either growing season ($p > 0.05$).

The nitrogen content in tissues of *Carex lasiocarpa* ranged from 1.63% to 2.81% in 1993 and from 1.90% to 2.45% in 1994 (Table 4.4.). *Eriophorum vaginatum* tissue contained 1.75% N in June of 1994. *Carex lasiocarpa* tissue nitrogen concentrations decreased in all minerotrophic sites; however, *E. vaginatum* tissue nitrogen levels increased in the bog from late June to late August.

June C:N ratios of *Carex lasiocarpa* ranged from 16.27 to 27.23 in 1993 and from 19.18 to 23.80 in 1994. The C:N ratio of *Eriophorum vaginatum* in June was 25.17 (only determined in 1994) (Table 4.5.). The C:N ratios increased in all minerotrophic sites but decreased in the bog in 1993 and 1994 due to the changes in N tissue content.

Total phosphorus concentrations of *Carex lasiocarpa* ranged from 1,410.7 (0.14%) to 2,620.3 µg/g dry weight (0.26%) in June 1993 and from 1,628.4 (0.16%) to 2,626.3 µg/g dry weight in June 1994 (0.26%) (Table 4.6.). TP concentrations of *Eriophorum vaginatum* were 1,537.9 µg/g dry weight (0.15%) in June 1994.

Carex lasiocarpa

Fens

Carbon tissue levels ranged from 44.42% to 44.87% in 1993 and from 44.85% to 45.30% in June 1994 (Table 4.4.). These levels did not change significantly throughout the growing season, exhibiting less than a 1% deviation during either year ($p > 0.05$). Nitrogen tissue concentrations ranged from 1.76% to 2.15% in June 1993 and from 1.90% to 1.95% in June 1994 (Table 4.4.). During both years, these levels decreased consistently, but not significantly ($p > 0.05$). June C:N ratios ranged from 20.99 to 25.62 in 1993 and from 23.67 to 23.80 in 1994 (Table 4.5.). The C:N ratio increased in all fens throughout both growing seasons. The ORF and RSF exhibited significant C:N changes in 1993 and 1994, whereas the C:N ratio in the LSF only changed significantly in 1994 (all $p < 0.05$).

The LSF had lower nitrogen tissue content in late June in 1993 than either the ORF or the RSF. The latter two fens exhibited similar nitrogen tissue levels during June, 1993 (Table 4.4.). In 1994, *Carex lasiocarpa* exhibited similar June tissue nitrogen levels in all three fens. During both years of this study, tissue nitrogen levels in *C. lasiocarpa* decreased to similar concentrations in all three fens by late August, although the early fall tissue N levels were slightly higher in 1993 than in 1994 (Table 4.4.). This means that the nutrient-poorer tissues lost proportionally less nutrients than the nutrient-richer plant tissues, explaining the significant changes in %N and consequently C:N ratios in the ORF and RSF in 1993 and 1994 and in the LSF only in 1994. Thus, it would appear that as plant tissue nitrogen levels increase, significantly larger quantities of N leach out of plant tissues throughout the growing season.

TP tissue concentrations ranged from 1,410.7 (0.14%) to 1,929.6 μg/g dry weight (0.19%) in 1993 and from 1,628.4 (0.16%) to 2,034.2 μg/g dry weight (0.20%) in 1994 (Table 4.6.). These levels decreased in all fens but significantly only in the RSF in 1993 and 1994 ($p < 0.05$). *Carex lasiocarpa* in the RSF exhibited the highest TP tissue concentrations in both years of this study. I speculate that this led to the proportionally larger decreases of TP from *C. lasiocarpa* compared to the TP tissue concentration decreases observed in the other two fens.

Carbon, nitrogen and phosphorus tissue concentrations from *Carex* spp. are rare in the literature. Chapin III et al. (1988) determined that *Carex biglowii* in the Alaskan tussock tundra had N and TP concentrations of 1.02% and 0.58% in August, respectively. Values for the same parameters reported by Small (1971) for *Carex tenuiflora* were higher for N (1.65%) and lower for TP (0.11%) in two bogs in early to mid-July near Ottawa, Canada. Differences in total phosphorus tissue concentrations can in part be explained by the different ecosystems in which the herb grew (tussock tundra versus bogs), different surface water concentrations of nutrients and the different *Carex* spp. examined. Rates of decomposition and nutrient mineralization differ among ecosystems, nutrient requirements vary among different *Carex* spp. and nutrients leach at varying rates from different plants, possibly even from plants of the same genus.

Marshes

The carbon content of *Carex lasiocarpa* tissues in June ranged from 43.48% to 44.93% in 1993 and from 43.85% to 43.86% in 1994 (Table 4.4.). Carbon content decreased slightly in both marshes in 1993 and 1994, although these changes were not significant ($p > 0.05$). The nitrogen content of tissues in June ranged from 1.63% to 2.81% in 1993 and from 2.02% to 2.45% in 1994 and decreased during both growing seasons (Table 4.4.). However, the only significant decrease occurred in the riverine marsh (RM) in 1993 ($p < 0.05$). June C:N ratios ranged from 16.27 to 27.23 in 1993 and from 19.19 to 22.31 in 1994 (Table 4.5.). These ratios increased significantly in both marshes in 1993 and 1994 ($p < 0.05$).

TP tissue concentrations in June ranged from 1,690.3 (0.17%) to 2,620.3 µg/g dry weight (0.26%) in 1993 and from 2,392.9 (0.24%) to 2,626.3 µg/g dry weight (0.26%) in 1994 (Table 4.6.). In both marshes, these levels decreased in 1993 and 1994, although the decrease was significant only in the LM in 1994 ($p < 0.05$).

Kistritz et al. (1988) examined nutrient tissue concentrations of *Carex lyngbyei* in a Fraser River tidal marsh, British Columbia. They found that both %N and %TP tissue levels decreased in aboveground tissues and increased in belowground tissues towards the end of the growing season. Auclair (1977) determined %N and %TP tissue levels of several *Carex* spp. in marshes near Lake St. Francis, Quebec. He reported N and TP tissue concentrations ranged from 0.842% to 1.153% and from 0.0907% to 0.1325%, respectively. The *Carex lasiocarpa* of my study contained substantially higher levels of both nutrients.

Auclair (1977) determined that *Carex* spp. N and P tissue concentrations are positively correlated to the stem density of the stand. He suggested that with a high stem density each plant would have relatively higher tissue nutrient concentrations. Plants growing in a high stem density environment require smaller quantities of carbon-rich tissues for structural support; however, plants growing in a low stem density environment require larger quantities of carbon-rich tissues since they do not have the structural support from neighboring plants. Auclair's (1977) results are supported by this study. Even though stand densities were not determined in this study, I assume that they correlate positively with NPP. TP and N tissue concentrations in June increased as production increased within the LM, RSF and LSF from 1993 to 1994. In the RM, the total NPP decreased from the first to the second year, as did the tissue nutrient concentrations. However, not all of these changes were significant from 1993 to 1994.

Eriophorum vaginatum in the bog

The carbon content of this sedge was 43.96% in late June and it increased by 2.66% to 46.56% by late August (Table 4.4.). Similarily, nitrogen tissue levels increased from 1.75% to 2.13% over the same time period (Table 4.4.). The C:N ratio decreased from 25.17 in late June to 22.21 in late August (Table 4.5.). The June TP tissue concentration was 1,537.9 µg/g dry weight (0.15%) and it decreased to 1,178.9 µg/g dry weight (0.12%) by late August (Table 4.6.). None of these changes were significant ($p > 0.05$).

Small (1971) reported that %N and %TP tissue concentrations in *Eriophorum vaginatum* in the Mer Bleue and Proulx bogs near Ottawa, Ontario, were 1.5% to 2.1% and 0.11 to 0.14% in early to mid-July, respectively. Also, Chapin III et al. (1988) found that *E. vaginatum* had N and TP tissue concentrations of 1.14% and 0.28% in late August near Everett pond, Alaska, respectively. Lechowicz & Shaver (1982) reported that %N tissue levels decreased from June to August at Eagle Creek, Alaska. When comparing the results of these previous studies to mine, it appears that N tissue concentrations in this species are independent of latitude. Small's (1971) results are comparable to both mine and Chapin III et al.'s (1988). However, in all previous studies, the N tissue concentratrions decreased towards the end of the growing season, whereas in my bog they increased from late June to late August. This is possibly due to higher surface water nitrogen concentrations in this site compared to those of the other studies. The increase in tissue N concentrations caused a decrease in the C:N ratio from late June to late August (Table 4.5.). Fertilization experiments showed that P caused the greatest increase in NPP, indicating that P, rather than N, is limiting growth of *E. vaginatum* in this site (see Chapter five). Therefore, tissue phosphorus concentrations will decrease before tissue nitrogen concentrations.

Lechowicz & Shaver (1982) determined that TP tissue levels decrease towards the end of the growing season. Although the TP tissue concentration in my bog increased from late June to late July, it had decreased substantially by late August and was substantially lower than those from Lechowicz & Shaver (1982). Even though the total phosphorus content in *Eriophorum vaginatum* may vary in magnitude among studies, these differences can partially be explained by different surface water nutrient concentrations of the different sites and the differing ecosystems (bogs versus tussock tundra). In all cases, the total phosphorus content in *E. vaginatum* tissues decrease towards the end of the growing season due to leaching and translocation of phosphorus from aboveground tissues.

Conclusions

Moss NPP exhibited greater variation among sites than between years, indicating the importance of climatic parameters for this stratum. Herb production varied significantly between years and among sites within each year and showed a significant positive correlation to the water level (mean r = 0.73). Shrub production only varied among sites each year and showed a significant negative correlation to the water level (mean r = -0.74). The bog exhibited the only significant tree cover of all sites but this stratum did not provide a notable contribution towards total NPP. Climatic variables, such as mean annual temperature, GDD and precipitation during the growing season, had the most notable effect on moss growth. Shrubs and herbs seemed to respond primarily to water level fluctuations rather than climatic variables.

Vascular plant NPP in fens related best to surface water concentrations of SRP (r = 0.80) and TP (r = 0.67) in 1993 and 1994, respectively. Total plant NPP in fens related best to NO_3^- (r = 0.85) and TP (r = 0.75) in 1993 and 1994, respectively. Marsh vascular and total plant NPP related best to alkalinity (r = 0.87) in 1993 and to SRP (r = 0.92) in 1994. The hypothesis that a higher water level relative to the peat surface will lead to a higher NPP was only partially supported. The bog had the lowest water level but an equally high or higher plant NPP than the fens. However, both the bog and the fens exhibited significantly lower production values than the marshes in this study. The results of this study support hypothesis one but refute hypothesis two. The site with the highest water level did exhibit the highest plant NPP but mean annual water levels were not the dominant factor in explaining plant production in the fens and marshes.

Tissue concentrations of C, N, TP and the C:N ratio in *Carex lasiocarpa* exhibited similar trends in the fens and marshes during 1993 and 1994. The carbon tissue concentrations remained unchanged, whereas %N and %TP decreased from late June to late August. Consequently, the C:N ratio in this herb increased during the same period. The stand density of *C. lasiocarpa* may determine tissue nutrient concentrations. In the site with the highest NPP and presumably the highest stand density, *C. lasiocarpa* exhibited the highest tissue nutrient concentrations of N and TP. Therefore, larger quantities of N and TP leached out of or were translocated from the aboveground plant tissues during the fall when compared to sites with lower stand densities and lower *C. lasiocarpa* tissue nutrient concentrations. Generally, tissue nutrient concentrations of N and TP in *C. lasiocarpa* were similar among the fens and marshes in late June and late August and followed a similar trend of decreasing tissue nutrient content during 1993 and 1994. However, TP tissue concentrations in *C. lasiocarpa* were substantially higher in the marshes than in *C. lasiocarpa* in the fens and *Eriphorum vaginatum* in the bog in June, 1994.

Tissue nutrient concentrations of *Eriophorum vaginatum* showed a variable response pattern. The nitrogen tissue concentrations increased from late June to late August (the C:N ratio decreased), whereas TP tissue levels decreased over the same period. Fertilization experiment revealed that P may limit growth of this herb in the bog (see Chapter five), possibly explaining lower TP levels in this species in the bog compared to those found in the same species in other bogs and the Alaska tussock tundra.

Therefore, hypotheses three and four were partially disproved, the nutrient status of a peatland is not the most dominant factor affecting plant tissue nutrient concentrations, plant community characteristics influence these nutrient variables as well.

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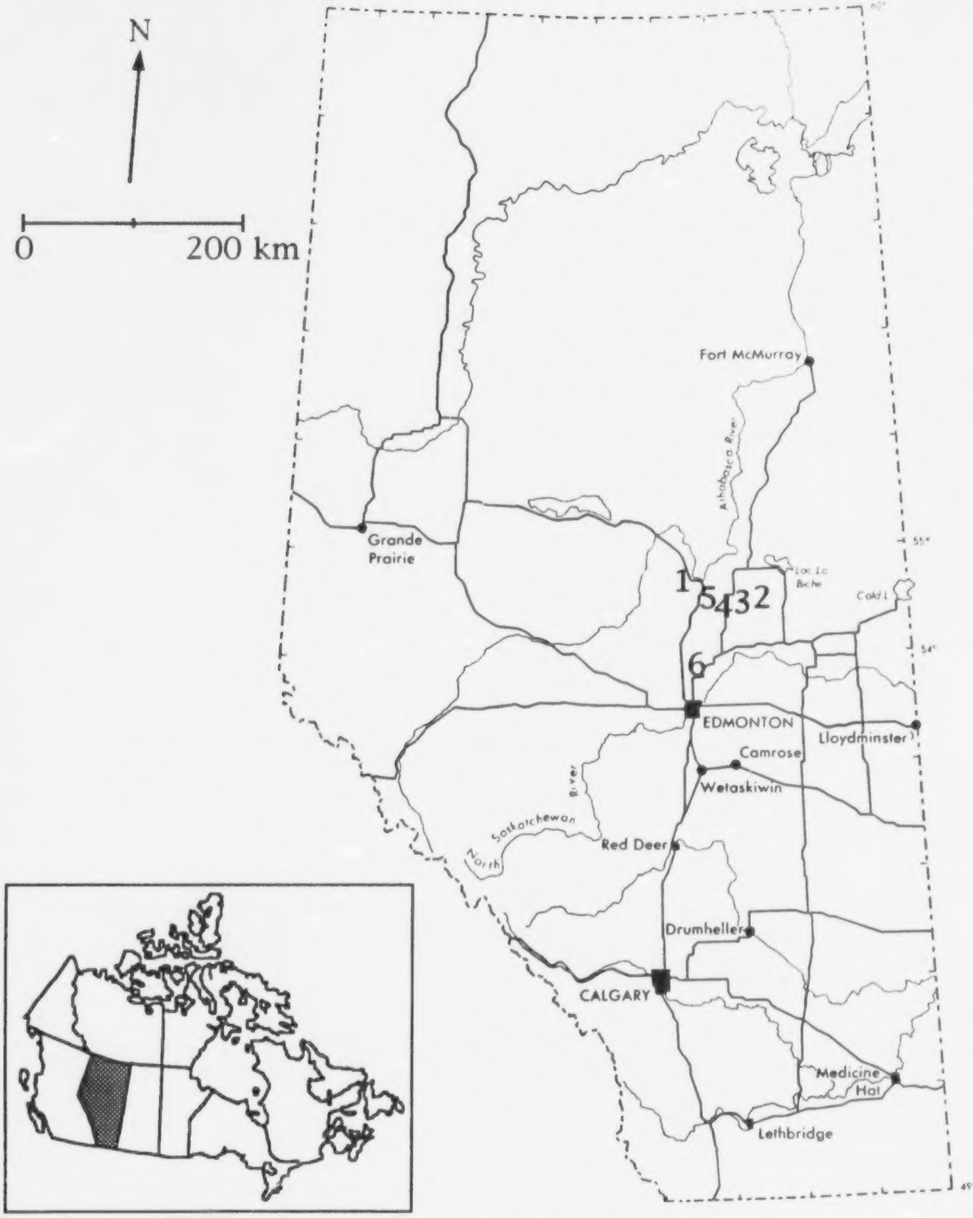
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200 km
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Fort McMurray
Athabasca River
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Lac La Biche
Cold L.
54°
6
EDMONTON
Lloydminster
Camrose
Wetaskiwin
North Saskatchewan River
Red Deer
Drumheller
CALGARY
Medicine Hat
Lethbridge
49°

Figure 4.1. Relative location of the six peatlands in central Alberta (**1** = bog, **2** = open rich fen, **3** = riverine sedge fen, **4** = lacustrine sedge fen, **5** = riverine marsh, **6** = lacustrine marsh).

Table 4.1 Means (ranges) of surface water parameters in six peatlands (bog, ORF = open rich fen, RSF = riverine sedge fen, LSF = lacustrine sedge fen, RM = riverine marsh, LM = lacustrine marsh) in 1993 and 1994

Characteristic	**Bog**	**ORF**	**RSF**	**LSF**	**RM**	**LM**
pH	3.89 (3.38 - 4.12)	6.23 (5.51 - 7.37)	7.10 (6.34 - 8.06)	6.98 (6.20 - 7.77)	7.44 (6.74 - 8.37)	7.37 (6.62 - 8.08)
* Corrected conductivity (µS)	7.8 (0 - 43.5)	74.7 (51.0 - 86.0)	231.0 (128.0 - 342.0)	197.2 (57.0 - 286.0)	432.8 (293.0 - 717.0)	780.3 (651.0 - 1186.0)
Alkalinity (mg/L CaCO3)	0 --	27.3 (12.5 - 39.6)	99.4 (55.8 - 167.5)	75.2 (19.5 - 136.3)	201.1 (75.0 - 299.25)	242.3 (77.8 - 380.1)
HCO3- (mg/L)	0 --	33.2 (15.2 - 48.3)	121.1 (67.8 - 204.2)	91.7 (23.8 - 166.1)	243.6 (91.4 - 364.9)	295.4 (94.8 - 463.4)
NO3- (ug/L)	6.9 (2.0 - 16.6)	6.6 (1.4 - 36.0)	7.5 (1.8 - 44.2)	5.6 (0.7 - 20.7)	7.9 (2.3 - 19.7)	24.3 (2.8 - 233.2)
NH4+ (µg/L)	29.4 (0.8 - 202.0)	35.9 (1.7 - 144.7)	16.7 (1.7 - 109.9)	32.3 (0.2 - 469.9)	299.0 (2.2 - 2274.9)	431.7 (3.6 - 3515.9)
TDN (µg/L)	1185.2 (629.1 - 2303.8)	1184.9 (935.8 - 1781.0)	1072.2 (664.9 - 1836.6)	1027.1 (612.7 - 1594.0)	1619.6 (404.6 - 6251.0)	2648.8 (1537.0 - 5633.0)
SRP (µg/L)	20.1 (2.5 - 75.4)	8.7 (2.7 - 20.6)	20.8 (3.0 - 93.2)	4.4 (.08 - 13.6)	36.0 (2.0 - 114.3)	161.0 (8.7 - 867.1)
TDP (µg/L)	58.5 (23.3 - 132.3)	29.1 (12.7 - 42.0)	39.2 (12.7 - 99.6)	19.4 (9.3 - 46.0)	59.2 (2.9 - 116.8)	206.8 (22.7 - 1145.5)
TP (µg/L)	110.1 (36.6 - 297.3)	99.3 (34.2 - 528.8)	143.4 (17.6 - 461.4)	57.1 (13.0 - 196.9)	312.5 (97.2 - 1013.9)	433.0 (79.4 - 1864.0)
Na+ (mg/L)	1.4 (0.78 - 2.20)	2.4 (2.1 - 2.6)	2.8 (3.0 - 2.6)	4.8 (1.7 - 7.4)	7.8 (2.6 - 12.9)	33.6 (3.2 - 64.0)
Ca2+ (mg/L)	3.1 (0 - 19.80)	9.4 (7.6 - 13.8)	17.9 (15.2 - 20.6)	21.4 (7.2 - 50.5)	47.4 (29.5 - 64.4)	54.8 (43.2 - 66.4)
Mg2+ (mg/L)	1.2 (0 - 7.80)	6.4 (4.1 - 8.7)	8.3 (7.1 - 9.4)	8.4 (2.6 - 25.6)	14.3 (11.1 - 17.5)	11.1 (0 - 22.3)
1993 Water table depth (cm)	-39.6 (-28.1 - -49.8)	-4.2 (-7.1 - -1.3)	7.9 (5.7 - 11)	-2.8 (-12.7 - +4.7)	32.4 (18.9 - 50.2)	-22.0 (-33.0 - -6.4)
1994 Water table depth (cm)	-44.5 (-32.9 - -51.2)	-3.2 (-10.1 - +4.5)	7.6 (-8.1 - +26.9)	19.6 (6.4 - 27.5)	-11.2 (-14.7 - +17.3)	22.8 (13.6 - 40.1)
* Depth of oxidation (cm)	27.5 (22.3 - 30.36)	9.8 (7.4 - 13.05)	5.4 (2.5 - 7.4)	3.9 (2.43 - 5.73)	13.5 (9.76 - 15.96)	** **

* measured only in 1994
** peat was completely anoxic

TDN = total dissolved nitrogen
SRP = soluble reactive phosphorus
TDP = total dissolved phosphorus
TP = total phosphorus

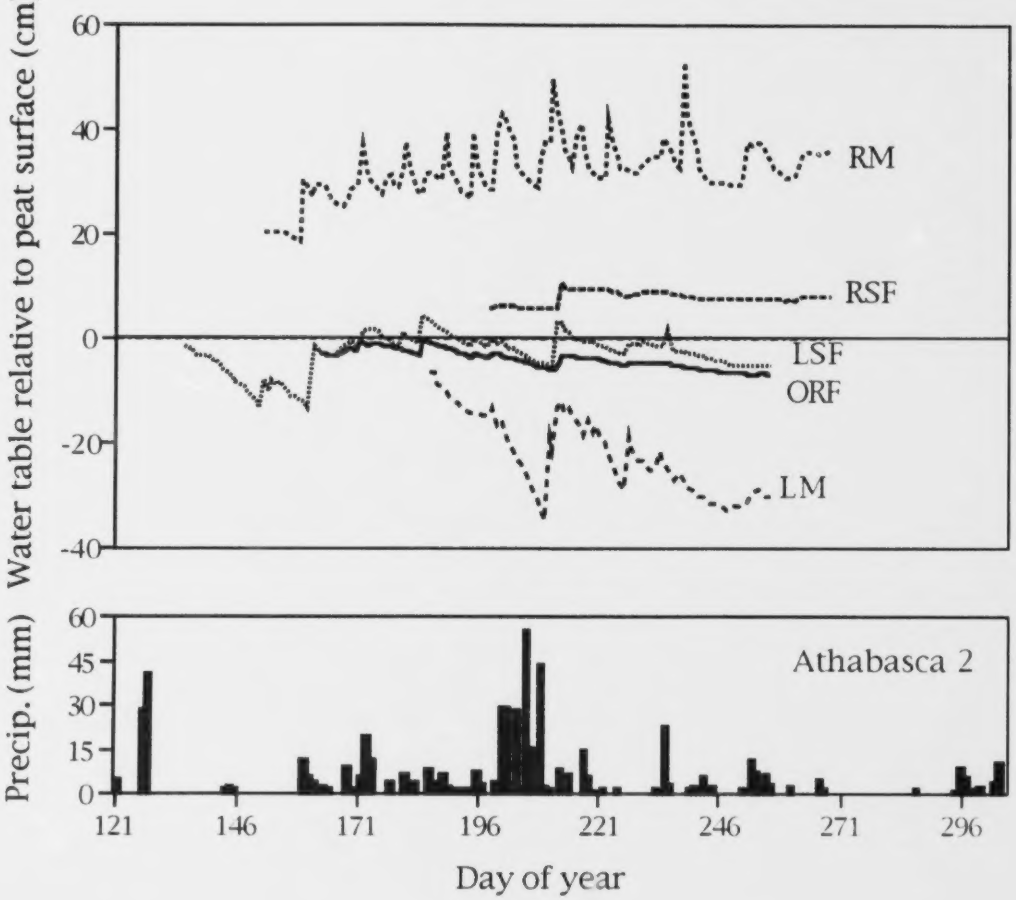

Figure 4.2. Water level fluctuations relative to peat surface (0 cm) in five peatlands (ORF = open rich fen, LSF = lacustrine sedge fen, RSF = riverine sedge fen, RM = riverine marsh, LM = lacustrine marsh) during the 1993 growing season compared to daily precipitation at the nearby weather station (Athabasca 2).

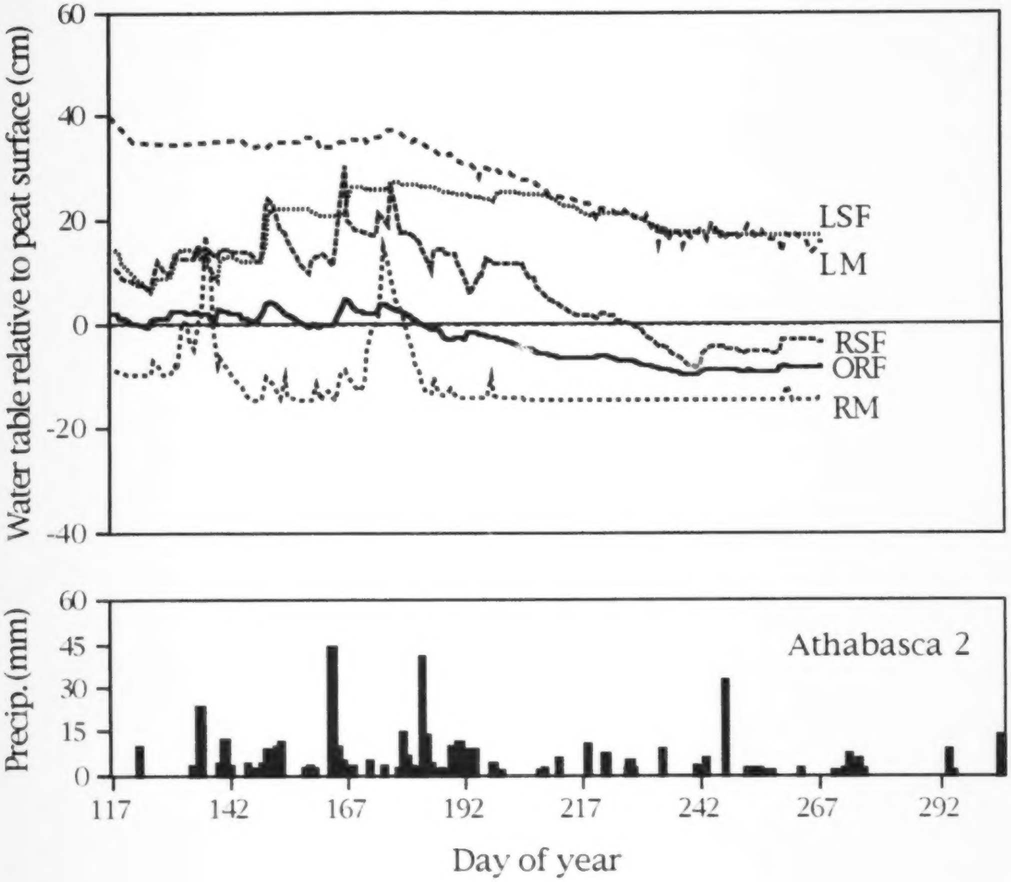

Figure 4.3. Water level fluctuations relative to peat surface (0 cm) in five peatlands (ORF = open rich fen, LSF = lacustrine sedge fen, RSF = riverine sedge fen, RM = riverine marsh, LM = lacustrine marsh) during the 1994 growing season compared to daily precipitation at the nearby weather station (Athabasca 2).

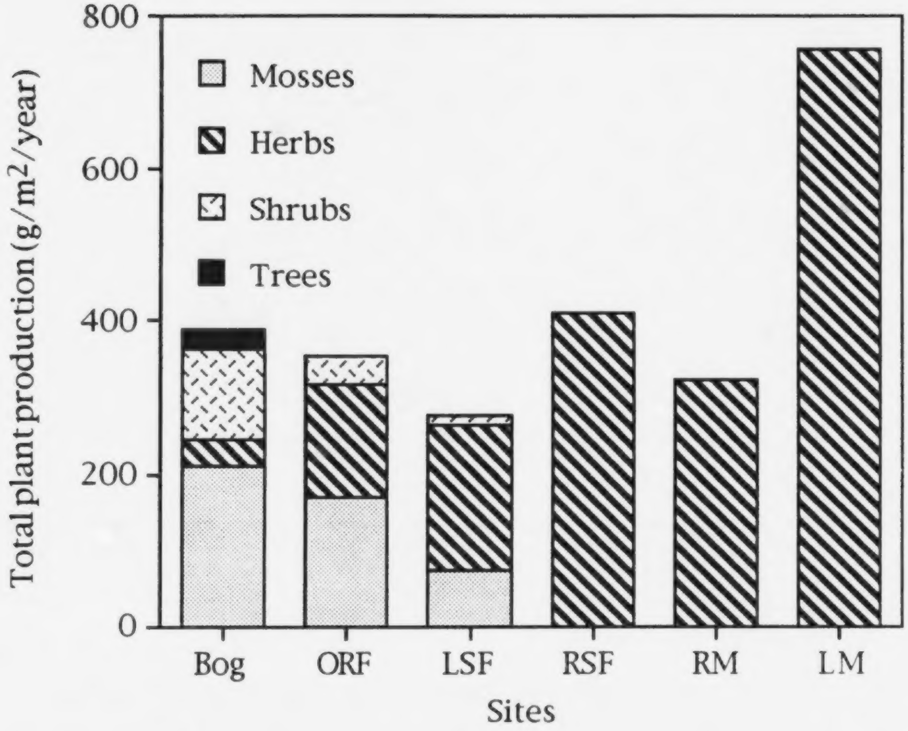

Figure 4.4. Comparison of total aboveground plant production in six peatlands (bog, ORF = open rich fen, LSF = lacustrine sedge fen, RSF = riverine sedge fen, RM = riverine marsh, LM = lacustrine marsh). Bars represent means of 1993 and 1994, except for the bog, which was sampled only in 1994. Estimated tree production (where applicable) was based on mean five year growth increments (Szumigalski & Bayley, under review).

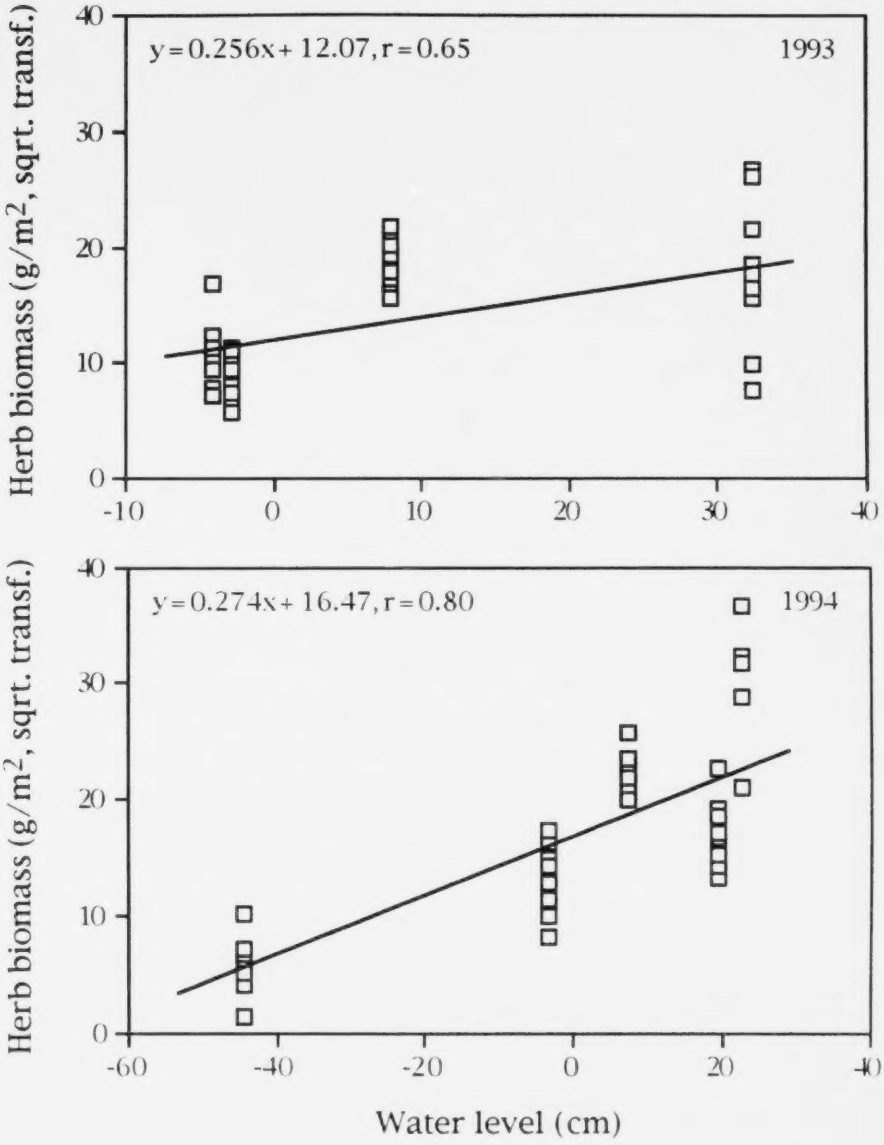

Figure 4.5. Peak herb aboveground biomass (square-root transformed) in relation to the mean site water level relative to the peat surface (0 cm). Symbols represent harvested quadrats from four (open rich fen, lacustrine sedge fen, riverine sedge fen, riverine marsh) and five (bog, open rich fen, riverine sedge fen, lacustrine sedge fen, lacustrine marsh) peatlands in 1993 and 1994, respectively.

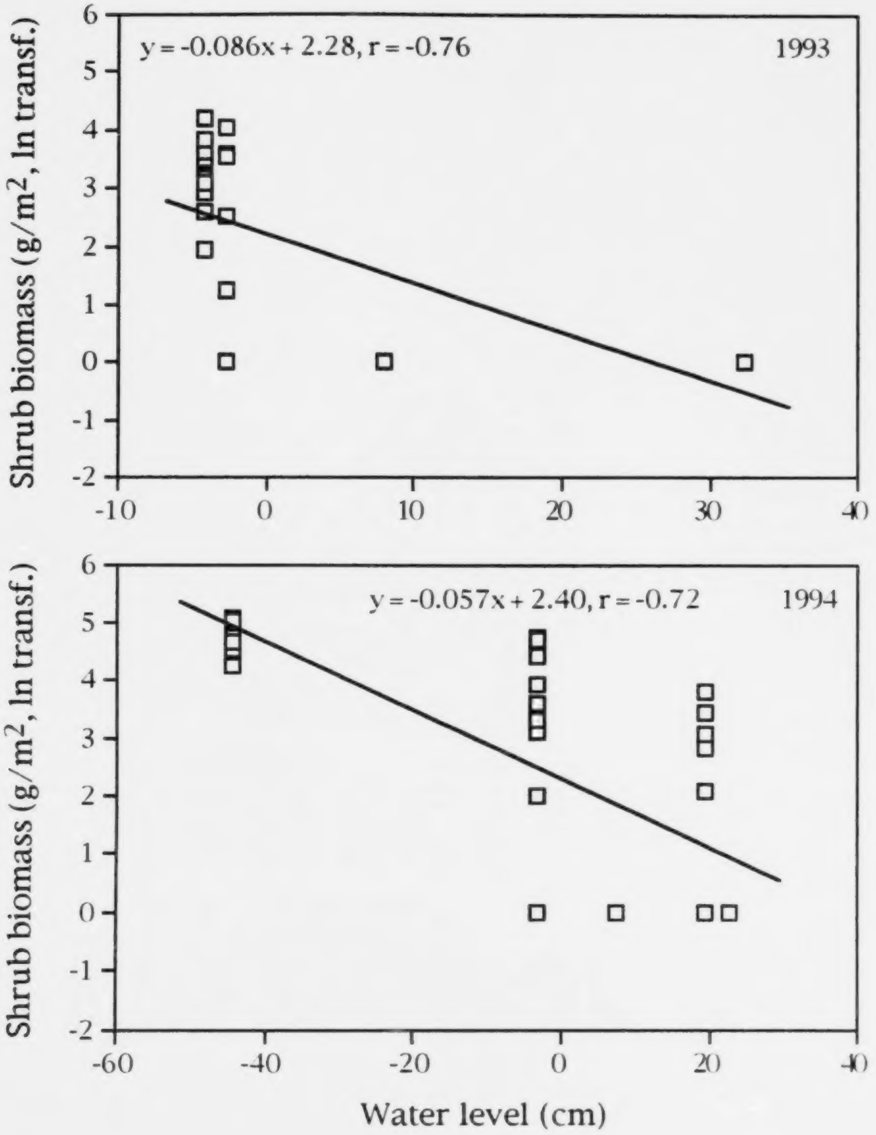

Figure 4.6. Peak shrub terminal aboveground biomass (new leaves and stems) (natural-log transformed) in relation to the mean site water level relative to the peat surface (0 cm). Symbols represent harvested quadrats from four (open rich fen, lacustrine sedge fen, riverine marsh, lacustrine marsh) and five (bog, open rich fen, lacustrine sedge fen, riverine marsh, lacustrine marsh) peatlands in 1993 and 1994, respectively.

Table 4.2. Correlation coefficients of vascular and total plant productivity (vasc. and tot. prod.) with various surface water chemistry parameters in five peatlands (fens: open rich fen, lacustrine sedge fen, riverine sedge fen; marshes: riverine marsh, lacustrine marsh) in 1993 and 1994.

Type		1993			1994		
		Parameter	**r**	**p**	**Parameter**	**r**	**p**
Fens	**Vasc. prod.**	SRP	0.80	**	TP	0.67	*
		NO3-	0.53	**	NO3-	0.65	**
		TDN	0.24	*			
		TDP	0.13	**			
	Tot. prod.	NO3-	0.85	**	TP	0.75	*
		SRP	0.40	*	TDP	0.43	*
		pH	0.30	*			
Marshes	**Vasc. and tot. prod.**	Alkalinity	0.87	*	SRP	0.92	*

* 0.05 > p > 0.01
** 0.01 > p > 0.001

SRP = soluble reactive phosphorus
TP = total phosphorus
TDP = total dissolved phosphorus
TDN = total dissolved nitrogen

Table 4.3. Correlation coefficients of vascular and total plant productivity with various surface water chemistry parameters in five peatlands (open rich fen, lacustrine sedge fen, riverine sedge fen, riverine marsh, lacustrine marsh) in 1993 and 1994.

	1993			1994		
NPP	**Parameter**	**r**	**p**	**Parameter**	**r**	**p**
Vascular	Adj. Cond.	0.80	***	SRP	0.76	**
	NO3-	0.53	**	TDN	0.39	*
	NH4+	0.24	*			
	pH	0.20	*			
Total	Adj. Cond.	0.78	***	SRP	0.69	**
	NO3-	0.48	**	TDN	0.46	*
	NH4+	0.30	**			

* 0.05 > p > 0.01
** 0.01 > p > 0.001
*** 0.001 > p > 0.0001

SRP = soluble reactive phosphorus
TDN = total dissolved nitrogen
Adj. Cond = adjusted conductivity
NPP = net primary production

Table 4.4. Mean (+/- SE) percent nitrogen and carbon of the dominant plant species (bog = Eriophorum vaginatum, all other sites = Carex lasiocarpa) in six peatlands (bog, ORF = open rich fen, RSF = riverine sedge fen, LSF = lacustrine sedge fen, RM = riverine marsh, LM = lacustrine marsh) in 1993 and 1994. The bog was sampled only in 1994.

Site	1993						1994					
	June 26 % C	July 26 % C	Aug. 26 % C	June 26 % N	July 26 % N	Aug. 26 % N	June 26 % C	July 26 % C	Aug. 26 % C	June 26 % N	July 26 % N	Aug. 26 % N
Bog	-- --	-- --	-- --	-- --	-- --	-- --	43.96 (2.48)	46.34 (0.10)	46.56 (0.28)	1.75 (0.06)	1.90 (0.05)	2.13 (0.14)
ORF	44.42 (0.23)	44.73 (0.15)	43.86 (0.47)	1.93 (0.08)	1.90 (0.08)	1.59 (0.06)	44.87 (0.37)	44.69 (0.33)	45.08 (0.29)	1.90 (0.10)	1.53 (0.08)	1.26 (0.07)
RSF	44.47 (0.35)	45.25 (0.08)	44.93 (0.15)	2.15 (0.15)	1.71 (0.08)	1.47 (0.03)	45.30 (0.26)	45.36 (0.19)	45.60 (0.27)	1.95 (0.15)	1.28 (0.07)	1.30 (0.07)
LSF	44.87 (0.12)	44.85 (0.04)	44.84 (0.14)	1.76 (0.07)	1.60 (0.08)	1.54 (0.04)	44.85 (0.11)	45.02 (0.11)	45.22 (0.20)	1.90 (0.08)	1.47 (0.08)	1.30 (0.06)
RM	44.93 (0.09)	45.20 (0.29)	44.47 (0.14)	2.81 (0.20)	2.18 (0.15)	1.74 (0.15)	43.85 (0.44)	44.44 (0.31)	43.09 (0.13)	2.45 (0.36)	2.33 (0.14)	2.08 (0.19)
LM	43.48 (0.29)	43.21 (0.35)	42.90 (0.17)	1.63 (0.12)	1.66 (0.19)	1.21 (0.12)	43.86 (0.11)	43.30 (0.66)	43.66 (0.48)	2.02 (0.19)	1.80 (0.16)	1.23 (0.10)

Table 4.5. Mean (+/- SE) C:N ratios of the dominant plant species (bog = Eriophorum vaginatum, all others = Carex lasiocarpa) in six peatlands (bog, ORF = open rich fen, RSF = riverine sedge fen, LSF = lacustrine sedge fen, RM = riverine marsh, LM = lacustrine marsh) in 1993 and 1994. The bog was sampled only in 1994.

	1993			1994		
Site	**June 26 C:N**	**July 26 C:N**	**Aug. 26 C:N**	**June 26 C:N**	**July 26 C:N**	**Aug. 26 C:N**
Bog	-- --	-- --	-- --	25.17 (0.63)	24.47 (0.60)	22.21 (1.60)
ORF	23.16 (0.90)	23.72 (0.95)	27.67 (1.14)	23.77 (1.25)	29.54 (1.56)	36.20 (2.07)
RSF	20.99 (1.62)	26.63 (1.20)	30.66 (0.65)	23.67 (1.99)	35.96 (2.24)	35.45 (1.97)
LSF	25.62 (1.07)	28.22 (1.33)	29.24 (0.80)	23.80 (1.32)	30.94 (1.60)	35.15 (1.68)
RM	16.27 (1.23)	21.07 (1.65)	26.22 (2.36)	19.18 (3.02)	19.31 (1.25)	21.23 (1.94)
LM	27.23 (2.11)	27.08 (3.09)	36.55 (3.10)	22.31 (2.11)	24.75 (2.72)	35.89 (3.18)

Table 4.6. Comparison of TP (total phosphorus, ug/g) content of two plant species in six peatlands (bog, ORF = open rich fen, RSF = riverine sedge fen, LSF = lacustrine sedge fen, RM = riverine marsh, LM = lacustrine marsh) in 1993 and 1994. The bog was sample only in 1994.

		1993			1994		
Site	**Species**	**June**	**July**	**August**	**June**	**July**	**August**
Bog	*Eriophorum vaginatum*	--	--	--	1,537.9	1,697.8	1,178.9
ORF	*Carex lasiocarpa*	1,410.7	1,416.7	1,220.9	1,628.4	1,521.4	1,164.2
RSF	*Carex lasiocarpa*	1,929.6	1,829.4	1,417.8	2,034.2	1,556.9	1,368.5
LSF	*Carex lasiocarpa*	1,566.6	1,364.2	1,349.2	1,902.8	1,424.7	1,323.6
RM	*Carex lasiocarpa*	2,620.3	2,177.3	1,488.2	2,392.9	2,196.1	1,806.8
LM	*Carex lasiocarpa*	1,690.3	1,673.2	1,559.6	2,626.6	2,134.9	1,298.3

5. RESPONSE OF NET PRIMARY PRODUCTION TO NITROGEN AND PHOSPHORUS FERTILIZATION IN PEATLANDS IN BOREAL ALBERTA.

Introduction

It is generally believed that nitrogen (N), phosphorus (P) and potassium (K) are the most limiting nutrients in peatlands (Reader, 1978; Mitsch & Gosselink, 1993). Organic soils generally have large amounts of P and N tied up in organic forms but these nutrients may be unavailable to plants and thus limiting to plant growth (Mitsch & Gosselink, 1993).

A number of studies examined the effects of nutrient fertilization on the net primary production (NPP) of specific plant species. Simms (1987) and Loach (1968) examined the effects of nutrient fertilization on ericaceous peatland species, whereas Shaver & Chapin III (1980) and Lechowicz & Shaver (1982) investigated the effects of artificial nutrient additions on six tundra species in Alaska. Bayley et al. (1987) fertilized a *Sphagnum* spp. dominated peatland to examine the effects on moss growth in northwestern Ontario.

It has been shown that different peatland species respond differently to nutrient fertilization (Loach, 1968; Lechowicz & Shaver, 1982; Simms, 1987). Deciduous shrubs are thought to respond quickly to added nutrients because of their high nutrient losses in senesced leaves each fall. Conversely, ericaceous shrubs, with their long-lived leaves and relatively low growth rates, should not respond as quickly as deciduous shrubs to fertilization (Chapin III, 1988). However, Shaver & Chapin III (1980) and Chapin III (1988) determined that deciduous and ericaceous shrubs responded positively after nutrient fertilization within one growing season in the Alaskan tussock tundra. Bartsch (1993) showed that production responses may also be delayed and the effects of fertilization may not be significant until the following growing season(s). Bartsch (1993) also noted that fertilization with different elements may answer the question of which nutrient limits plant growth in peatlands.

This fertilization study will focus on two questions: (1) Does N or P limit non-vascular and vascular plant growth in southern boreal Albertan peatlands and (2) how do the major plant species in these Alberta peatlands respond to nutrient fertilization. I hypothesize that either N or P is the limiting elemental nutrient in Alberta peatlands. By comparing the peak total aboveground production of N or P fertilized plots to that of unfertilized plots will indicate which elemental nutrient caused the greatest increase in NPP. The one resulting in the greatest increase in NPP compared to the control plots is the most limiting one to plant growth in these sites. Also, I hypothesize that deciduous shrubs and herbs will show a greater response to N or P fertilization than ericaceous shrubs due to their life history.

Study area and site descriptions

The five study sites which were fertilized in 1994 represent the range of peatlands present in Alberta, Canada. These included a bog, a riverine sedge fen (RSF), a lacustrine sedge fen (LSF), a riverine marsh (RM) and a lacustrine marsh (LM). The bog is located north of Bleak Lake at 54° 41' N and 113° 28' W, while the LSF (54° 28' N, 113° 19' W) and the RSF (54° 28' N, 113° 18' W) are located east of Perryvale. The RM is located northwest of Perryvale at 54° 28' N and 113° 23' W, and the LM is located northeast of Clyde (54° 10' N, 113° 34' W) (Figure 5.1.).

Mild summers and cold, snowy winters characterize the climate of central Alberta (Vitt et al., in press). The long term mean annual temperature is 1.7 °C (Environment Canada, 1982) and the total mean precipitation is approximately 500 mm for all sites. Appendix 1 summarizes the climatic data for the 1993 and 1994 growing periods for all sites. All five peatlands lie within the Boreal Forest Region of Canada (Rowe, 1972). Vascular plant nomenclature follows Packer (1983), whereas "brown" moss nomenclature follows Anderson et al. (1990) and *Sphagnum* nomenclature is in accordance with Anderson (1990).

Bog

The bog is a large, raised ombrotrophic island with 5 m of peat within a large peatland complex. The peat surface is raised about 0.3-0.5 m above an adjacent poor fen water track. The peat is arranged in large, dry hummocks which are separated by intermittent wetter hollows. The pH of the open water in the hollows ranged from 3.7 to 4.1. A sparse tree layer of *Picea mariana* (Mill.) BSP. covers about 25% of the wooded part of this bog. *Ledum groenlandicum* Oeder dominates the ericaceous shrub layer (covers about 75%) while the sparse herb stratum consists primarily of *Smilacina trifolia* (L.) Desf.. *Sphagnum fuscum* (Schimp.) Klinggr. comprises about 90% of the moss layer. Szumigalski & Bayley (under review) studied this site in 1991 and 1992.

Lacustrine Sedge Fen

This site is a large expanse of sedge dominated peatland situated aside a large body of water (approximately 62 ha) in a former north-south drainage channel (Vitt et al., in press) with 2-2.5 m of peat. This fen's topography is mainly flat with the occasional small hummock (about 5% of the peatland surface). The lacustrine sedge fen was largely inundated with water for most of 1991, characteristic of a marsh, but began to dry out in 1992; therefore, Vitt et al. (in press) classified this peatland as an extreme-rich fen. In 1993, this site continued to dry out, but in 1994 it was once again flooded, possibly due to beaver dams blocking outflows of the former drainage channel. The pH of the surface water ranged from 6.1 to 6.9. The vascular vegetation stratum consists primarily of *Carex lasiocarpa* Ehrh.. Shrubs comprise only about 5% of the peatland cover and consist mostly of *Salix pedicellaris* Pursh. The moss stratum is discontinuous and dominated by *Drepanocladus aduncus* (Hedw.) Warnst. in wet pools and by *Aulacomnium palustre* (Hedw.) Schwaegr. on top of dry hummocks. Szumigalski & Bayley (under review), who studied this site in 1991 and 1992, referred to this fen as 'sedge fen'.

Riverine Sedge Fen

This peatland is part of an extensive wetland complex adjacent to the aforementioned lacustrine sedge fen and has an approximate peat depth of 1 m. The pH of the surface water ranged from 6.3 to 8.1 during 1993 and 1994. It receives water from a discrete inflow at the southern end, and the outflow at the northern end controls the water level elevation. The water level was above the peat surface during the 1993 and 1994 growing seasons. In the spring of 1994, a constructed dam blocked the outflow and, as a result, the water level was substantially higher during the second growing season. The vascular vegetation stratum is dominated by *Carex aquatilis* Wahlenb., mosses are very sparsely distributed and shrubs are absent.

Riverine Marsh

This site is located on the floodplain of Tawatinaw River. During 1993, this marsh was periodically inundated with water and the water table was consistently above the peat surface. In 1994, a beaver dam just above the study area retained much of the stream flow and the water table dropped well below the peat surface. The pH of the surface water ranged from 7.1 to 8.4 and the peat is less than 1 m deep. The vascular vegetation layer is dominated by *Carex aquatilis* Wahlenb., during spring and early summer, but *Calamagrostis canadensis* (Michx.) Beauv. and *C. inexpansa* A. Gray were dominant during late summer and early fall. During their period of vegetation domination, these species cover about 95% of the surface. A number of other herb species are present, but they are only sparsely distributed. There are no moss and shrub strata present.

Lacustrine Marsh

This marsh is situated on the northwestern shore of Wakomao Lake (approximately 360 ha). Water flows into this lake from a drainage basin to the north (approximately 7800 ha) and from an artesian well area along the southwestern shore (approximately 300 ha). Water leaves through a small creek at the southern tip of

Wakomao Lake. During 1993, the water table was below the peat surface, but in 1994, this site was flooded with water, possibly due to beaver dams or man made dams blocking the outflow(s) of Wakomao Lake. The lake receives secondarily treated wastewater from Clyde (population < 1000) each spring and additional nutrients from agricultural run-off. No moss and shrub strata exist and the vascular vegetation layer is dominated by *Carex aquatilis* Wahlenb. and *Typha latifolia* L.. Together these two species cover approximately 80% of the surface. The peat depth is 1.5-1.75 m and the pH of the surface water ranged from 7.1 to 8.1.

Methods

Fertilization

Within the fens and marshes, two 5 x 50 m (250 m^2) plots were set up parallel to those investigated for vascular and non-vascular plant production. Within the bog, three 2 x 10 m (60 m^2 total area) plots were set up adjacent to the treeless 250 m^2 plot which was also examined for vascular and non-vascular plant productivity. Wooden stakes were used to indicate 1 m^2 sub-plots which would be fertilized with either nitrogen or phosphorus. These stakes were 10 m apart in both fens and both marshes and 2 m apart in the bog to achieve a non-fertilized buffer zone between adjacent fertilized sub-plots. Nitrogen or phosphorus fertilizer was applied to the same five randomly assigned sub-plots within each site in early June, early July and early August.

Nitrogen (N), in the form of granular NH_4NO_3, was applied to each site in three applications of 43.29 g/m^2 to obtain a loading rate of 15.0 g $N/m^2/year$. Phosphorus (P), in the form of granular P_2O_5, was applied to each site in three applications of 8.59 g/m^2 to achieve a loading rate of 2.14 g $P/m^2/year$. This results in a nitrogen to phosphorus ratio of 7:1, which corresponds with the Redfield ratio of these two elements in tissues of aquatic plants (Wetzel, 1983). The granular N or P fertilizers were evenly distributed over each sub-plot by hand. Since the bog is dry, in comparison to the other four peatlands, each fertilizer was crushed to a fine powder in the laboratory, dissolved in 100 mL of 2d-H_2O over night and further diluted with water indigenous to the bog (collected from a hollow adjacent to the established plots) to a total volume of 2 L before being applied to the vegetation.

All herbaceous and deciduous plant material was clipped at ground level in late August (when the unfertilized plots were harvested), dried at 48 ^{o}C and then sorted into live and dead matter. The dead matter was discarded and the live matter was further sorted into individual taxa and weighed to the nearest 0.1 g. Moss production in the bog was determined via the cranked wire method (Clymo, 1970). Twenty wires were set up in each sub-plot in late May, 1994, and total moss growth was measured in late August. Production of the herb, shrub and moss strata was determined as outlined in Chapter two.

Statistical analyses

ANOVAs were performed to determine the effects of N or P fertilization on non-vascular (bog) and vascular plant aboveground production (bog, riverine sedge fen, lacustrine sedge fen, riverine marsh, lacustrine marsh). Dunnett's tests were performed to make pairwise comparisons between the water (bog), N and P (all other sites) treatments against the controls.

ANOVAs also served to examine the effects of fertilization on specific plant species and vegetation groups (herbs, deciduous and ericaceous shrubs) within sites and Tukey tests were performed to make pairwise comparisons following significance from the ANOVAs. All statistical analyses were performed on SAS (SAS Institute Inc., 1989).

Results and discussion

Fertilization with nitrogen (N) or phosphorus (P) did not result in a significant increase in vascular plant production in any site ($p > 0.05$) (Figure 5.2.). However, non-vascular plant production in the bog increased significantly after the addition of water alone ($p < 0.0001$), resulting in a significantly higher total plant production compared to the control transect and those transects fertilized with dissolved N or P ($p < 0.0001$). The fens and marshes exhibited no significant increases in total NPP.

Bog

Non-vascular and total plant production increased significantly with the addition of water ($p < 0.0001$ and $p < 0.01$, respectively). Vascular plant production remained unchanged ($p > 0.05$) (Figure 5.2.). While the total herb production increased significantly ($p < 0.05$), the total deciduous and ericaceous shrub productions did not ($p > 0.05$). Moss production in this bog may primarily be limited by water, whereas total vascular plant production may not be limited strictly by either N or P, but possibly by a combination of nutrients.

Vascular plant production

The two dominant herbs, *Eriophorum vaginatum* and *Smilacina trifolia*, generally showed an increase in production with the addition of fertilizers or water, although, these increases were not significant in all cases (Table 5.1.).

Eriophorum vaginatum production did not change significantly after the addition of N (NPP of 7.4 $g/m^2/year$), P (NPP of 17.5 $g/m^2/year$) or water (NPP of 6.7 $g/m^2/year$) ($p > 0.05$) although NPP did increase compared to the control (3.6 $g/m^2/year$) (Table 5.1.). Shaver & Chapin III (1980) reported an increase in the shoot mass of approximately 12 to 15% of this herb after fertilizing with N, P or K in the Alaskan tussock tundra. Furthermore, their results indicate a larger increase in NPP after the application of both N and P fertilizers. Application of P fertilizer resulted in the largest, yet insignificant, increase in production of *E. vaginatum*. Vasander (1982) also found that *E. vaginatum* exhibited an increased NPP after the application of N and P fertilizers in a Finnish bog.

In this study, *Smilacina trifolia* NPP increased significantly with the addition of N and water alone ($p < 0.05$) but not with P compared to the control (Table 5.1.). Production increased from 6.1 g/m^2/year (control) to 14.3 g/m^2/year (N) and 16.2 g/m^2/year (water).

The only deciduous shrub with a substantial ground cover was *Salix pedicellaris* and its production did not change significantly ($p > 0.05$). Mean production values were 3.6 g/m^2/year (control), 7.5 g/m^2/year (N), 7.9 g/m^2/year (P) and 4.2 g/m^2/year (water) (Table 5.1.).

The four most prominent ericaceous shrubs were *Ledum groenlandicum*, *Andromeda polifolia*, *Oxycoccus quadripetalus* and *Vaccinium vitis-idaea*. No consistent response pattern in plant NPP emerged after the addition of fertilizers or water (Table 5.1.).

Ledum groenlandicum production decreased with the addition of N, P and water (Table 5.1.). Addition of fertilizer and water caused a production decrease from 65.1 g/m^2/year (control) to 48.9 g/m^2/year (N), 42.9 g/m^2/year (P) and 36.7 g/m^2/year (water). These decreases were significant at $p < 0.01$, 0.01 and 0.001, respectively. Shaver & Chapin III (1980) reported similar decreases in *Ledum* spp. growth after fertilizing with N or P in the Alaskan tussock tundra at Eagle Creek; however, their decreases were not as substantial as mine.

Andromeda polifolia production increased significantly with the addition of N (from 19.8 g/m^2/year (control) to 61.5 g/m^2/year) ($p < 0.05$), but not with the application of P or water. Vasander (1982) found that N and P fertilizers together caused this ericaceous shrub to increase production in a raised Finnish bog.

Oxycoccus quadripetalus production decreased significantly with the addition of N and water but not P. NPP values in this study changed from 10.9 g/m^2/year (control) to 1.6 g/m^2/year (N) ($p < 0.05$) and to 0.8 g/m^2/year (water) ($p < 0.05$).

Vaccinium vitis-idaea production did not change significantly ($p > 0.05$). Shaver & Chapin III (1980) also reported no change or only a small decrease in the production of this species in Alaska.

Altogether, herb production did not change significantly due to the addition of fertilizer or water, even though individual species exhibited significant NPP changes. This may be due to the large standard error (SE) terms in association with small sample sizes ($n = 5$ for the fertilization treatments). Also, the changes of production were not uniform across the ericaceous shrub species examined. *Ledum groenlandicum* and *Oxycoccus quadripetalus* exhibited a decrease in production due to the addition of some or all of the fertilizers, whereas *Andromeda polifolia* showed positive responses to the addition of N. It is theorized that some species have traits which allow them to grow in nutrient-poor habitats and that these same traits preclude them from becoming established in nutrient-rich ecosystems (Chapin III, 1980). However, Simms (1987) showed that species growing in nutrient-poor habitats responded differentially to nutrient additions. He showed that some shrubs may be better adapted to respond to nutrient fertilization than others. In support, Bartsch (1993) showed that the ericaceous shrub, *Chamaedaphne calyculata*, produced a three-fold increase in biomass within the first year of receiving fertilizers in Caribou Bog, Maine.

Chapin III et al. (1986) determined that soil microbes and fungi readily immobilize N and P fertilizers in Alaska, making these nutrients unavailable to plants. Chapin III (1988) also showed that some peatland species may exhibit "luxury consumption" of nutrients. This provides nutrients that can be used for future growth, especially in the spring, and the absorption and storage of nutrients would make them inaccessible to competing plant species (Schulze & Chapin III, 1987). It is possible that the added N or P was immobilized shortly after application. Some species utilized them immediately for increased growth, while others may have stored them for future use.

Non-vascular plant production

Fertilizing with N or P resulted in a non-significant decrease in production of *Sphagnum fuscum* from 164.5 g/m^2/year (control) to 105.2 g/m^2/year (N) and 160.7 g/m^2/year (P) ($p > 0.05$). Water addition caused *S. fuscum* production to increase significantly to 437.7 g/m^2/year ($p < 0.0001$) (Table 5.1.).

Vasander (1982) reported that *Sphagnum fuscum* NPP decreased after the combined application of N and P fertilizers in a Finnish raised bog. Vasander (1982) and Reinikainen & Lindholm (1980) attributed this to salting shock, especially after the application of urea as a nitrogen source. However, I did not observe any indication of salting on *S. fuscum* in this site. Hillman et al. (1990) and Vasander (1982) both showed that *Sphagnum* spp. growth is inhibited under dry conditions; therefore, water, rather than N or P, may be the most limiting parameter in this bog. Verhoeven & Schmitz (1991) also found that addition of water to mosses increased their production in a mid-successional fen with groundwater discharge in the Netherlands. However, their increases were not significant.

It is conceivable that fertilization would increase vascular plant production which in turn would shade the understorey moss species. In this bog, *Smilacina trifolia* increased its production by 234% and 266% after applying N or water, respectively. This herb is characterized by broad leaves (Packer, 1983) and possibly shaded the *Sphagnum fuscum* plants beneath. Hayward & Clymo (1983) determined that light is an important factor affecting the growth of *Sphagnum* spp. and a decrease in light intensity could result in a decrease in *Sphagnum* spp. growth. Therefore, added nutrients were more beneficial for the vascular plant strata than for the moss stratum, which appeared to be water limited.

Fens and marshes

There were generally no significant increases in vascular plant production in any of the fens and marshes after the addition of N or

P fertilizers ($p > 0.05$) (Figure 5.2.). In the lacustrine sedge fen, *Carex* spp. exhibited a significant increase in NPP after the application of N (from 293.8 g/m^2/year (control) to 368.1 g/m^2/year) ($p < 0.05$) (Table 5.1.). However, total herb production did not increase substantially since other herb species did not respond significantly after the application of N or P fertilizer. In the riverine sedge fen, total herb production decreased after fertilizing with N or P but these changes were also not significant ($p > 0.05$).

In the marshes, total herb production generally increased after the addition of fertilizers, but these increases were also not significant. In the lacustrine marsh, herb production increased from 932.7 g/m^2/year to 1,376.5 g/m^2/year after applying N (Table 5.1.). This increase was not significant due to the small sample size and the very large SE of the N fertilized quadrats ($n = 3$). In the riverine marsh, *Carex* spp. and *Calamagrostis canadensis* also exhibited substantial changes after the addition of fertilizers but these changes were not significant either ($p > 0.05$) (Table 5.1.).

Fertilization studies in various minerotrophic peatlands showed that water levels as well as fertilizer loading rates affect the magnitude of plant growth responses. Verhoeven & Schmitz (1991) fertilized three fens in the Netherlands and found that a mid-successional fen with groundwater discharge and one with surface water inflows were N limited. A late-successional fen with groundwater discharge was P limited. Bayley et al. (1985) reported no significant increases in total production in a marsh near Claremont, Florida, after applying P at low annual loading rates. However, at higher loading rates, vascular production increased. Also, Kadlec (1987) listed the effects of sewage application on the total production in a number of wetlands, all showing substantial increases in NPP after the addition of nutrients. Conversely, Schwartz & Gruendling (1985) examined the effects of nutrient additions to a riverine marsh in Steven's Brook, Vermont, and reported no significant increases in NPP of *Typha* sp. and *Scirpus* sp.. They determined that phytoplankton and bacteria increased significantly in biomass and that the additional nutrients were ultimately transported downstream.

In marshes, water level fluctuations are just as important as nutrient concentrations in affecting vegetation production (Bayley et al., 1985). At high water levels, anoxic conditions in the peat result in the release of P and the retention of N. Under oxic peat conditions, the converse holds true (Bayley et al., 1985). The nutrient loading rates in my study may have been too low to cause a significant increase in plant production in these fens and marshes. Also, since the water levels fluctuated in both marshes, alternating anoxic and oxic peat conditions may have released P and N in sufficient quantities to stimulate plant growth throughout the growing season. This may have masked the effects of fertilization. Barko & Smart (1978, 1986) and Neely & Davis (1985) suggested that production in freshwater marshes is limited by N, high water levels and subsequent anoxic peat condition could lead to a release of P but not N into the water column. Although poorer in surface water nutrients, the two fertilized fens of this study also did not exhibit significant increases in vascular plant production. The ambient mean total NH_4^+ and NO_3^- peat concentrations (top 12 cm) were 1.56 g/m^2 in the marshes, 0.77 g/m^2 in the fens (both in the summer of 1993) and 0.15 g/m^2 in the bog (in the summer of1992). Thus, loading rates were sufficiently high to elicit a significant vegetation response in the bog but not in the fens and marshes, possibly due to previously discussed environmental characteristics of these sites, microbial immobilization of the fertilizers or physiological differences of the plant species.

Furthermore, antecedent NO_3^- within the surface water of these sites may have increased denitrification losses by inhibiting fermentative bacteria involved in the reduction of NO_3^- to NH_4^+ (Cole, 1988) and increase the activities of NO_3^- reductase (Firestone, 1982) and dissimilatory NO_2^- and N_2O reductases (Korner et al., 1987). Thus, rates of denitrification will increase and limit nitrogen assimilation into plant tissues.

Simms (1987) reported that different shrubs, although closely related, respond differently to elevated nutrient levels. The life history of individual species determines how and when responses to fertilization will occur. Furthermore, the effects of fertilization may be long term and changes in the species composition of an ecosystem may have beneficial consequences for one species and deleterious effects for another (Vasander, 1982).

Caution is necessary when comparing fertilization studies as a number of variables change: (1) loading rates may vary, (2) a fertilizer is often added in conjunction with another fertilizer or several others, (3) herbs and shrubs reach their maximum biomasses at different times of the year; therefore, sampling both strata at the same time may underestimate one and overestimate the other (Shaver & Chapin III, 1980; Vasander, 1982), (4) production in hollows and hummocks often varies significantly within a site (Vasander, 1982) and (5) significant responses may not occur within the first year of fertilizer application (Simms, 1987).

Conclusions

Fertilizing the bog, two fens and two marshes with N or P (and water in the bog) only partially answered the questions of which nutrient limits plant production in peatlands in central Alberta. Thus, the first hypothesis was only partly proven. Vascular and total plant production in the fens and marshes did not increase significantly with the addition of either fertilizer. In the bog, non-vascular plant production increased significantly after the addition of water. Due to the dominance of the moss stratum in the bog, total plant production was also significantly increased after the addition of water. N or P did not affect non-vascular and vascular plant NPP within the bog.

Ambient total NH_4^+ and NO_3^- concentrations in the top 12 cm of the peat profile were suffiently low in the bog but too high in the fens and marshes to elicit a vegetation response. Fungi and other microorganisms may have immobilized the fertilizers which would render then unavailable to plants. Also, environmental characteristics of the fens and marshes and physiological attributes of the plant species may have masked immediate response patterns. Furthermore, NO_3^- in the surface waters may have favoured denitrification over nitrogen assimilation within these sites. It appears that moss production is limited by water, rather than N or P in the bog, whereas the vascular vegetation stratum was not limited by any one but possibly by a combination of elemental nutrients.

Different species responded differently to N or P fertilization within the five peatlands. Generally, herbs exhibited an increase in production after the addition of N but not P, ericaceous shrubs responded both positively and negatively and deciduous shrubs showed no response at all due to nutrient or water additions within the bog. In the fens and marshes, herb and deciduous shrub production showed variable responses to fertilization, but none of these were significant.

Responses to nutrient perturbations are species specific within southern boreal peatlands in Alberta. Comparing the results of this study to others, it appears that a latitudinal fertilization response gradient exists in peatlands in North America. At higher latitudes, vegetation responses are more pronounced due to the slow nutrient turnover. At lower latitudes, individual species respond in a similar fashion but the magnitudes of the responses are diminished. This may be due to higher rates of decomposition and nutrient mineralization rates. My second hypothesis was disproved as clear patterns of fertilization responses did not exist.

It was not possible to predict vegetation responses of herb, deciduous and ericaceous shrubs due to the addition of fertilizers in these peatlands. It is likely that these species co-evolved together to form a stable plant community. Individual species, rather than the growth forms (herbs, deciduous and ericaceous shrubs) compete against each other, therefore, individual species will respond differently due to nutrient perturbations.

Recent research has focussed on using wetlands to treat secondarily treated wastewater. It has been shown that certain wetland plant species are efficient in taking up nutrients from the water column, which is reflected in an increase in plant production. The peatlands of this study responded variably to the addition of N or P fertilizer. The bog exhibited the most significant changes in plant production, whereas the fen and marsh vegetation generally did not respond to nutrient addition at these loading rates.

Therefore, fens and marshes in Alberta are able to tolerate low loading rates of nutrients and could be used to treat secondarily treated wastewater.

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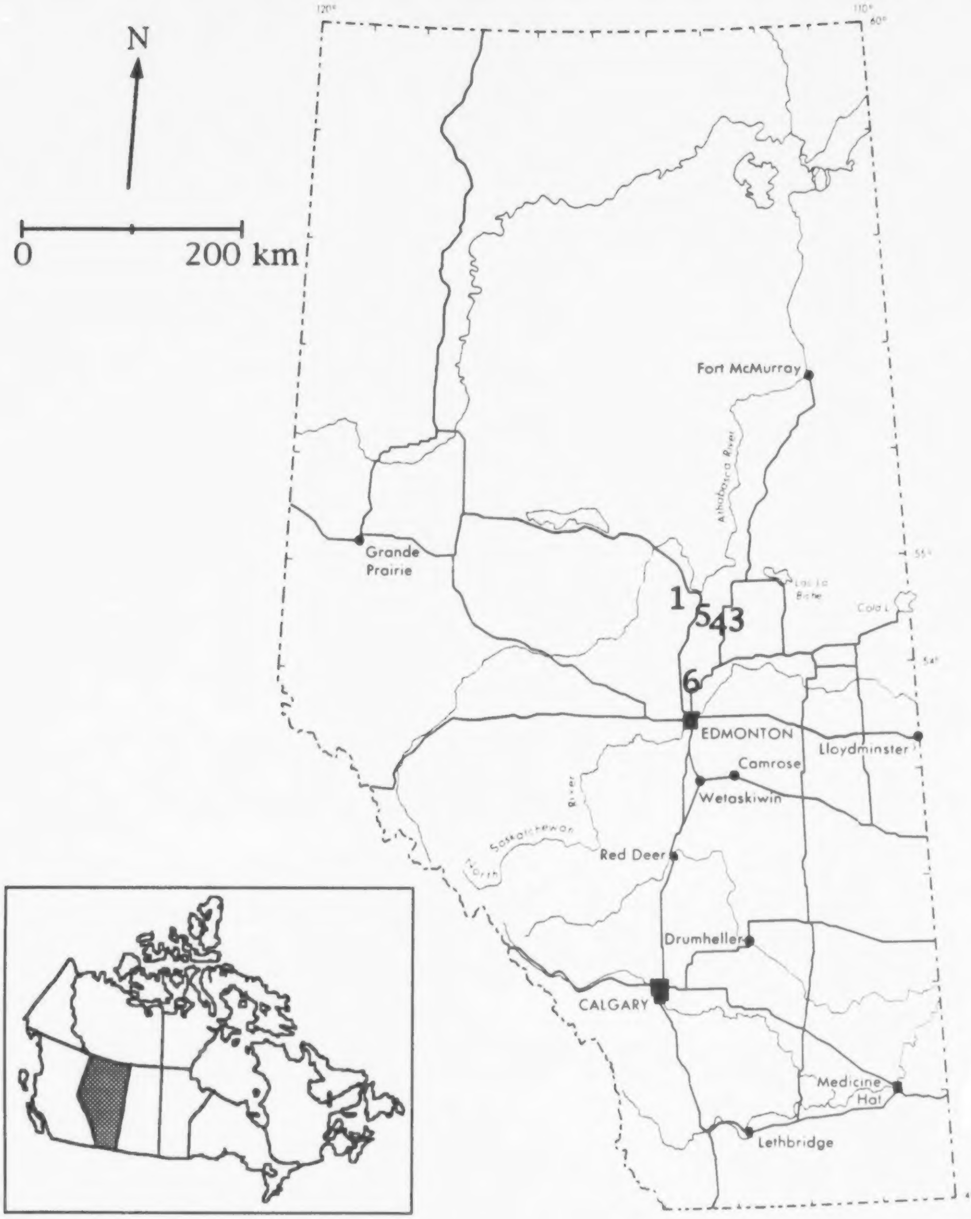
N
0
200 km
120°
110°
60°
Fort McMurray
Athabasca River
Grande Prairie
55°
Lac La Biche
Cold L.
1
5
4
3
6
54°
EDMONTON
Lloydminster
Camrose
Wetaskiwin
North Saskatchewan River
Red Deer
Drumheller
CALGARY
Medicine Hat
Lethbridge
49°

Figure 5.1. Relative location of the five peatlands in central Alberta (**1** = bog, **3** = riverine sedge fen, **4** = lacustrine sedge fen, **5** = riverine marsh, **6** = lacustrine sedge fen). These sites represent part of a larger group of peatlands currently under investigation.

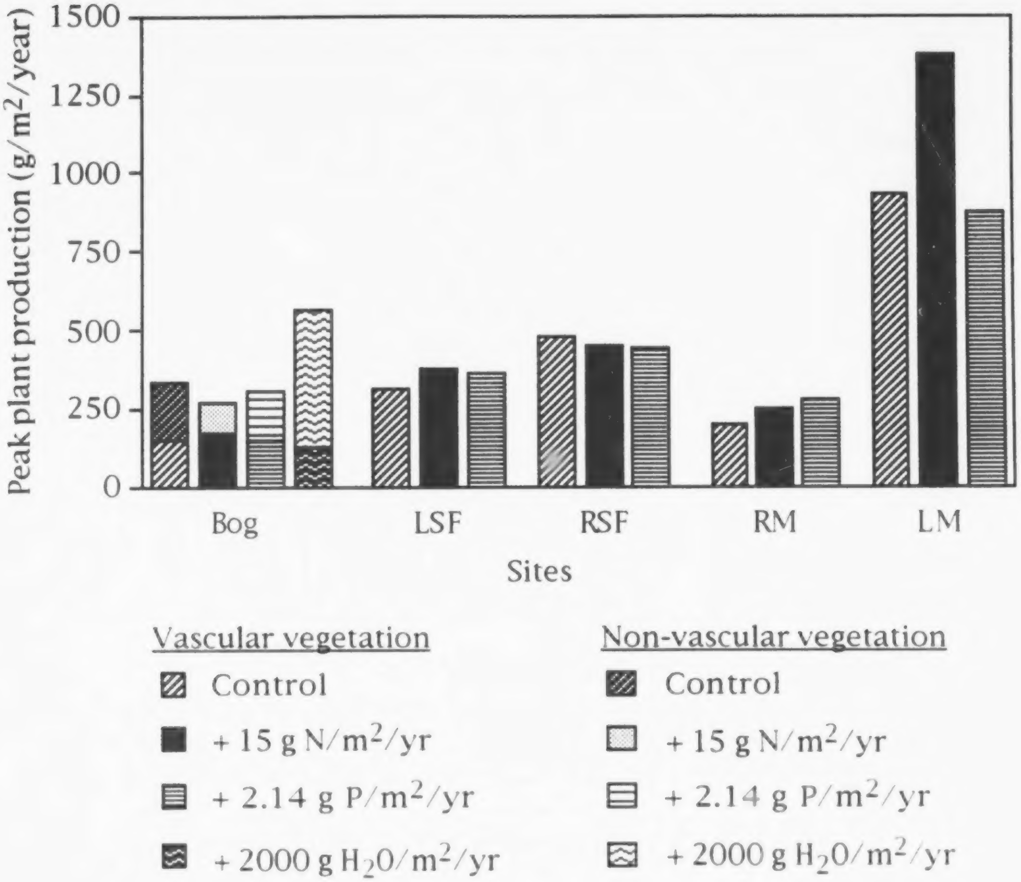

Figure 5.2. Effects of nitrogen (N) or phosphorus (P) fertilization on peak non-vascular (bog) and vascular aboveground plant production (g/m^2/year) (bog, LM = lacustrine marsh, LSF = lacustrine sedge fen, RSF = riverine sedge fen, RM = riverine marsh) in five peatlands in 1994.

Table 5.1. Effects of nitrogen (N), phosphorus (P) or water addition on the peak aboveground production (g/m^2/year) of species in five peatlands (bog, LSF = lacustrine sedge fen, RSF = riverine sedge fen, RM = riverine marsh, LM = lacustrine marsh) in 1994.

Site	**Species**	**Control**	**N**	**P**	**Water**
Bog	*Eriophorum vaginatum*	3.6	7.4	17.5	6.7
	Smilicina trifolia	6.1	14.3 *	9.1	16.2 *
	Salix pedicellaris	3.6	7.5	7.9	4.2
	Ledum groenlandicum	65.1	48.9 **	42.9 **	36.7 ***
	Andromeda polifolia	19.8	61.5 *	33.0	36.7
	Oxycoccus quadripetalus	10.9	1.6 *	6.3	0.8 *
	Vaccinium vitis-idaea	21.7	26.0	22.6	38.2
	Sphagnum fuscum	164.5	105.2	160.7	437.7 ****
LSF	*Carex* spp.	293.8	368.1 *	346.7	--
RSF	*Carex* spp.	474.6	451.7	440.3	--
RM	*Carex* spp.	93.9	216.2	170.9	--
	Calamagrostis canadensis	99.5	39.8	93.2	--
LM	*Carex* spp.	877.8	1376.5	872.5	--

* $0.05 > p > 0.01$
** $0.01 > p > 0.001$
*** $0.001 > p > 0.0001$
**** $0.0001 > p > 0.00001$

6. EFFECTS OF HYDROLOGIC CHANGES ON PRODUCTION AND SURFACE WATER CHEMISTRY IN TWO BOREAL PEATLANDS IN ALBERTA: IMPLICATIONS FOR GLOBAL WARMING.

Introduction

Peatlands are primarily northern ecosystems (Gore, 1983 a, b), whose total area is estimated to exceed 420 million hectares (ha) (Kivinven & Pakarinen, 1980; Sjörs, 1980). Approximately three quarters of all peatlands are in Canada and the former U.S.S.R., while the remainder is distributed over northern European countries (Kivinen & Pakarinen, 1980). In Canada, 12%, or approximately 111 million ha, of the country's land mass is covered by some type of peatland, most of it in the zone of discontinuous permafrost (Gorham, 1988).

Peatlands are defined as waterlogged ecosystems, where the water table is near or at the peat surface (Gorham, 1991), plant production exceeds the rate of decomposition (Zoltai, 1988), and the peat thickness is greater than 30-40 cm, depending upon which country's definition of peatlands is utilized (Gorham, 1991). The accumulated organic matter is very wet, and water usually comprises upwards of 90% of the volume below the peat surface (Clymo, 1983).

Most models used to predict ecosystem responses to global climate warming assume that the atmospheric carbon dioxide concentrations will double (2xCO_2) (Robock, 1993; Wigley & Jones, 1990). The vast majority of these models predict grassland and forest ecosystem responses and only recently have peatlands received any attention. The peatland models try to ascertain how bryophyte species will react under a 2xCO_2 climate scenario (Gignac et al., under review; Gignac & Vitt, 1994). Other models try to predict whether peatlands will be sinks or sources of carbon (C) under warmer climatic condition by measuring methane (CH_4) and CO_2 fluxes from peatlands (Moore, 1994; Yavitt et al., 1993; Roulet et al., 1993; Armentano & Menges, 1986). In comparison to the amount of research in forestry and grasslands, data documenting the responses of vascular plant species to climatic warming are scarce. Furthermore, the future of precipitation patterns under warmer climates are unclear: some models assume increases in precipitation, while others assume decreases (Intergovernmental Panel of Climate Change [IPCC], 1991, 1990). It is the general concensus that mean annual temperatures will increase between 3 and 5 °C and that the water table will drop as an indirect result of increased atmospheric temperatures in northern ecosystems (Gignac et al., under review; Gignac & Vitt, 1994; Manabe & Stouffer, 1993; Martikainen et al., 1993).

The hydrology of peatlands is influenced by climate, microtopography and surficial geology and plays a major role in peatland ecology (Chapin III et al., 1988) and biogeochemistry (Gorham, 1994). The degree of groundwater upwelling (Shedlock et al., 1993; Glaser et al., 1990) is expected to change under global warming (Gorham, 1994). This is predicted to result in alterations of the peatland microclimate, such as surface radiation, peat temperature regime and evapotranspiration. These microclimatic alterations affect plant growth, nutrient mineralization and emissions of trace gases, such as CO_2 and CH_4 (Dise et al., 1993).

Szumigalski & Bayley (under review (a), (b), (c)) and I have examined plant production, water level fluctuations and surface water chemistry parameters in a lacustrine sedge fen (LSF) and a bog from 1991 to 1994 (vascular plant production was not measured in the bog in 1993). This chapter is the compilation of four years of data on water level, plant production and some surface water chemistry parameters. The data are examined to provide an indication on how Alberta's southern boreal peatlands might react to atmospheric warming. I hypothesize that: (1) production of herbs and mosses will decrease as the water level drops, (2) production of shrubs will increase due to different environmental preferences of this plant stratum, (3) surface water nutrient concentrations will decline with a drop in the water level and (4) tissue nutrient concentrations will decrease with a drop in water level due to smaller quantities of nutrients in the surface water.

Study area and site descriptions

The bog is located north of Bleak Lake at 54° 41' N and 113° 28' W, while the lacustrine sedge fen (LSF) (54° 28' N, 113° 19' W) is located east of Perryvale (Figure 6.1.).

The climate of the area is characterized by mild summers and cold, snowy winters (Vitt et al., in press). Table 6.1. summarizes climatic variables for these two peatlands from the Athabasca 2 weather station (Environment Canada, 1982). Both peatlands lie within the Boreal Forest Region of Canada (Rowe, 1972). The "brown" moss and *Sphagnum* nomenclatures follow Anderson et al. (1990) and Anderson (1990), respectively, while that of the vascular plants follows Packer (1983).

Bog

The bog is a large, raised ombrotrophic island within a large peatland complex. The peat is 5 m thick and is raised about 0.3-0.5 m above an adjacent poor fen water track. The peat is arranged in large, dry hummocks, which are separated by intermittent wetter hollows. The pH of the open water in the hollows ranged from 3.7 to 4.1. A sparse tree layer of *Picea mariana* (Mill.) BSP. covers about 25% of the wooded part of the bog. *Ledum groenlandicum* Oeder dominates the ericaceous shrub layer (covers about 75%), while *Vaccinium vitis-idaea* L., *Oxycoccus microcarpus* Turcz. and *Andromeda polifolia* L. are also present. The sparse herb stratum consists of *Smilacina trifolia* (L.) Desf., *Rubus chamaemorus* L. and *Eriophorum vaginatum* L.. *Sphagnum fuscum* (Schimp.) Klinggr. comprises about 90% of the moss layer. *Sphagnum angustafolium* (C. Jens. *ex* Russ.) C. Jens. and *S. magellanicum* Brid. make up the remainder of this vegetation stratum on mid-hummocks while *Polytrichum strictum* Brid. can be found on dry hummocks.

Lacustrine Sedge Fen

This site is a large expanse of sedge dominated peatland situated aside a large body of water (approximately 62 ha) with 2-2.5 m of peat. This fen's topography is mainly flat with the occasional small hummock (about 5% of the peatland surface). Szumigalski & Bayley (under review (a)) referred to this site as 'sedge fen'. The lacustrine sedge fen was largely inundated with water for most of 1991, characteristic of a marsh, but the water level was below the peat surface in 1992 and 1993; therefore, Vitt et al. (in press) classified this peatland as an extreme-rich fen. In 1994 it was once again flooded, possibly due to beaver dams blocking outflows of a drainage channel. The pH of surface water ranged from 6.1 to 6.9. The vascular vegetation consists primarily of *Carex lasiocarpa* Ehrh. and *C. diandra* Schrank. Other species present are *C. chordorrhiza* L.f., *C. limosa* L. and *C. aquatilis* Wahlenb.. Shrubs comprise only about 5% of the peatland cover and consist exclusively of *Salix pedicellaris* Pursh and *Betula pumila* L. *var. glandulifera* Regel. The moss stratum is discontinuous and dominated by *Drepanocladus aduncus* (Hedw.) Warnst., *Hamatocaulis vernicosus* (Mitt.) Hedenäs and *Calliergon giganteum* (Schimp.) Kindb. in wet pools and by *Aulacomnium palustre* (Hedw.) Schwaegr. on top of dry hummocks.

Methods

A detailed outline of the methods employed to measure the net primary production of the moss, herb, shrub and tree strata are in Chapter two. Clymo's (1970) cranked wire method was employed to measure moss growth in the bog. Due to the microtopography of the LSF, the moss mat was harvested in quadrats and growth of the dominant species was determined from innate characteristics. Multiple harvests were performed in late June, late July and late August to measure production of the herb and shrub strata. Tree production was estimated from Szumigalski & Bayley (under review (a)).

The methods employed to collect and analyze water samples follows Szumigalski & Bayley (under review (c)) and those outlined in Chapter four. Water samples were collected from the same small depressions dug into the peat in monthly intervals in 1991 and 1992 and in bimonthly intervals in 1993 and 1994 during the ice-free season. Water samples were analyzed for nitrate (NO_3^-), ammonium (NH_4^+), soluble reactive phosphorus (SRP), total dissolved phosphorus (TDP), total phosphorus (TP), potassium (K^+), sodium (Na^+), calcium (Ca^{2+}), magnesium (Mg^{2+}), chloride (Cl^-), sulfate (SO_4^{2-}), pH, alkalinity, bicarbonate (HCO_3^-), and conductivity (adjusted for pH and temperature).

Environment Canada (1982) provided climatic data from the Athabasca 2 weather station, such as quantity and timing of precipitation, number of growing degree days and air temperature.

Water level fluctuations were measured with Steven's F water level recorders in the LSF from 1991 until 1994 (Szumigalski & Bayley, under review (c)). In the bog, a Steven's F water level recorder was set up in 1991 and 1992 (Szumigalski & Bayley, under review (c)); however, a permanently attached meter stick was used to monitor water level fluctuations in 1993 and 1994. The meter stick measurements were related to measurements from a pore water sampler, which was used to determine the relative position of the water table to the peat surface. The pore water sampler was also used to supplement meter stick and water level recorder measurements in the LSF.

The depth of oxidation was measured as outlined by Szumigalski & Bayley (under review (c)) in 1991 and 1992. Chapter four describes the methods used in the following two years. Steel welding rods were inserted into the peat and retrieved at monthly intervals. The distance from the peat surface to the lowest extent of rust on the rods was measured and assumed to be the depth of the acrotelm (oxygenated peat horizon). The methods for this technique follow those outlined by Bridgham et al. (1991).

Eriophorum vaginatum from the bog and *Carex lasiocarpa* from the LSF were selected for analyses of C, N, and TP tissue concentrations. Plant samples originated from quadrats clipped as part of my (Chapter two) and Szumigalski & Bayley's (under review (a)) production studies. Nitrogen (N) plant tissue concentrations were analyzed with a Model 440 Elemetary Analyzer (Control Equipment Corp.). Total phosphorus (TP) analyses followed the molybdophosphovanadate method outlined by Parkinson & Allen

(1975) and Prepas & Rigler (1982). Results were expressed as %N, C:N and %TP (or as µg/g dry weight).

Moss, herb and shrub production, amounts of precipitation, growing degree days (GDD) and air temperatures were analyzed with one-way ANOVAs to determine significant variations among and within years from 1991 to 1994. Tukey tests were used to make pairwise comparisons after the detection of significance from the ANOVAs. Total plant production could not be analyzed due to the differential responses of different vegetation strata to the same environmental variable (Szumigalski & Bayley, under review (c)). Multiple stepwise regressions (forward) were used to examine the relationship among surface water chemistry and climatic parameters and moss, herb and shrub production from 1991 to 1994. Autocorrelation analyses were performed for each surface water nutrient parameter to determine any correlation between successive samples within each site. Pearson correlation coefficients were determined among all surface water chemistry and climatic parameters within each site to establish if any of the nutrients or climate variables were correlated with each other.

Most statistical analyses were perfomed on SAS (SAS Institute Inc., 1989), except for the autocorrelation analyses, which were performed on SYSTAT (SYSTAT Inc., 1992).

Results and discussion

The effects of water level on plant production

Lacustrine sedge fen (LSF)

Production of herbs, primarily *Carex lasiocarpa*, ranged from 79.7 g/m^2/year (1993) to 300.0 g/m^2/year (1994) with intermediate NPP values in 1991 and 1992 (Figure 6.2.). Production of this stratum was significantly lower in 1993 than in 1994 ($p < 0.05$). Shrub production ranged from 7.0 g/m^2/year in 1992 to 14.3 g/m^2/year in 1994 (Figure 6.2.) and was not significantly different among years ($p > 0.05$). Production of *Drepanocladus aduncus* ranged from 26.8 g/m^2/year in 1993 to 120.8 g/m^2/year in 1994 (Figure 6.2.). NPP varied significantly between 1991 and 1992 ($p < 0.001$) and between 1993 and 1994 ($p < 0.05$) but not between 1992 and 1993 ($p > 0.05$). Total plant production ranged from 120.7 g/m^2/year in 1993 to 435.1 g/m^2/year in 1994 and varied significantly between 1993 and 1994 ($p < 0.05$).

Water level only correlated with herb ($r = 0.73$, $p < 0.001$) and shrub ($r = 0.22$, $p < 0.01$) production in the lacustrine sedge fen (LSF) from 1991 to 1994 (Table 6.2.).

A close relationship between water level and herb production in Alberta peatlands has previously been demonstrated by Szumigalski & Bayley (under review (c)) in 1991 ($r = 0.88$) and 1992 ($r = 0.83$) in a bog and five fens and in 1993 ($r = 0.65$) and 1994 ($r = 0.80$) in three fens and two marshes (Chapter four). Also, Laitinen (1990) showed that herbs, specifically *Carex* spp., are more tolerant of water saturated soils than shrubs. The mean growing season water level rose by 22.4 cm from 1993 to 1994 and herb production increased by 376% in the LSF. Szumigalski & Bayley (under review (c)) reported that a drop of 14 cm in the water level caused the herb NPP to decrease by 40% in the same site between 1991 and 1992.

Terminal shrub production in Alberta peatlands was negatively correlated with water levels ($r = -0.76$ in 1993, $r = -0.72$ in 1994) (Chapter four) and Szumigalski & Bayley (under review (c)) reported a similar relationship between these two variables ($r = -0.72$ in 1991, $r = -0.70$ in 1992). The results of this study seemingly contradict those findings as the correlation between water level and shrub production was positive ($r = 0.22$) in the LSF between 1991 and 1994. However, shrubs in this fen almost exclusively inhabit the drier hummocks and are rarely found growing in wet hollows and the correlation was weak. It has been demonstrated that shrub production is greater on hummocks than in hollows (Backéus, 1990; Wallén et al., 1988; Moore, 1989), as waterlogged soils inhibit oxygen absorption by shrub roots (Reader, 1978). The results of this study support those of Backéus (1990), Wallén et al. (1988) and Moore (1989).

The non-significant ($p > 0.05$) increase in shrub production observed over the four years of this study can be attributed to the larger size of the plants harvested. Larger individuals will have a greater productivity than smaller ones and a small increase in production from 1991 to 1994 can be expected.

Bog

Production of *Sphagnum fuscum* ranged from 119 g/m^2/year (1992) to 211 g/m^2/year (1994) and was significantly different between 1993 and 1994 ($p < 0.05$) (Figure 6.3.). Herb NPP ranged from 8.4 g/m^2/year in 1991 to 34.5 g/m^2/year in 1994 (Figure 6.3.) and was significantly higher in 1994 than in 1991 and 1992 ($p < 0.05$). Shrub production ranged from 76.8 g/m^2/year (1991) to 116.2 g/m^2/year (1994) and was not significantly different among years ($p > 0.05$) (Figure 6.3.). Total plant production in the bog increased from 235.0 g/m^2/year in 1991 to 389.9 g/m^2/year in 1994 (Figure 6.3.). Plant production of any stratum was not significantly correlated with water levels in the bog ($p > 0.05$) (Table 6.2.).

Results of this study show that herb and shrub production in the bog correlated best with surface water concentrations of NH_4^+ ($r = -0.81$, $p < 0.05$) and soluble reactive phosphorus (SRP) ($r = 0.84$, $p < 0.05$) (Table 6.2.). Even though the water level did not significantly affect moss, herb and shrub production in the bog from 1991 and 1994 ($p > 0.05$), the water level relative to the peat surface does influence the solubility of nutrients by affecting the redox potential of the peat. Under anoxic conditions, phosphorus solubility is enhanced, whereas nitrogen solubility is reduced. During the years with higher NH_4^+ surface water concentrations (1991 and 1992) (Table 6.3.), herb production was lower (Figure 6.3.). Ullrich et al. (1984) demonstrated that ammonium affected the electrical membrane characteristics in *Lemna gibba* Gl., which resulted in a reduced K^+ uptake rate into the roots of this aquatic herb. In addition, a transient NH_4^+-induced K^+ efflux from roots in sweet potatos has been reported by Munn & Jackson (1978). I speculate that a similar mechanism affected the herb species in the bog and that the effects of this mechanism were compounded by the low concentrations of K^+ in the surface water in those two years (Table 6.3.). This may have led to a K^+ deficiency and low herb production in the bog in 1991 and 1992. In 1994, ammonium concentrations in the surface water were substantially lower and K^+ concentrations were significantly higher, resulting in a diminished toxicity effect of ammonium on herb growth, and herb production increased significantly.

Surface water concentrations of SRP exhibited a strong positive correlation with shrub growth in the bog. SRP concentrations in the surface water did not vary significantly among years ($p > 0.05$), but they were substantially higher in 1992 and 1994 compared to 1991.

The effects of water level on surface water chemistry

Lacustrine sedge fen

The water level in the LSF ranged from a mean growing season mininum of -6.79 cm below the peat surface in 1992 to a maximum of 19.60 cm above the peat surface in 1994 and was significantly different between 1991 and 1992 and between 1993 and 1994 ($p < 0.05$) (Table 6.4.). The depth of oxidation was greatest during the driest year and smallest during the wettest year. The pH ranged from annual means of 6.43 to 7.01. Adjusted conductivity was significantly lower in 1991 and 1992 than in 1993 and 1994 ($p < 0.05$) and alkalinity and HCO_3^- were both significantly lower in 1992 and 1993 than in 1994 ($p < 0.05$). All other surface water chemistry parameters were similar during the four years of this study ($p > 0.05$) (Table 6.4.).

In the LSF, NO_3^- ($r = -0.45$) and Ca^{2+} ($r = 0.75$) surface water concentrations correlated best with water level fluctuations. As the water level dropped, NO_3^- surface water concentrations increased and those of Ca^{2+} decreased (Figure 6.4.).

If the water level and Ca^{2+} concentrations drop, herb production will decrease in the LSF. Calcium is a mineral involved in cell division, numerous enzymatic pathways and a deficiency of this mineral leads to the death of meristametic regions within shoots and roots of plants (Salisbury & Ross, 1985). Shrub production best related to NO_3^- surface water concentrations ($r = 0.86$) (Table 6.2.). A negative correlation between water level and NO_3^- surface water concentrations ($r = -0.45$, $p < 0.05$) (Figure 6.4.) indicates that shrub production may be enhanced. However, water and other nutrients, especially Ca^{2+}, may limit shrub NPP.

Bog

The water level fluctuated a maximum of 5 cm between years (Table 6.3.) but the mean annual water levels were not significantly different among years ($p > 0.05$). The lowest mean annual water level was measured in 1994 and the highest in 1993 with 1991 and 1992 mean annual water levels intermediate. The depth of oxidation paralleled the water level fluctuations, whereby greater depths of oxidations were observed in years with lower annual mean water levels (Table 6.3.). The pH ranged from annual means of 3.60 to 4.20 and adjusted conductivity, alkalinity and HCO_3^- were zero, due to the low pH in the bog. Potassium concentrations in the surface water were significantly greater in 1994 than in any of the preceeding three years ($p < 0.05$), whereas calcium concentrations were significantly lower in 1994 than in 1991 to 1993 ($p < 0.05$). The remaining surface water chemistry parameters were similar during the four years of this study ($p > 0.05$) (Table 6.3.).

In the bog, surface water concentrations of potassium (K^+) ($r = 0.94$, $p < 0.05$) and total dissolved phosphorus (TDP) ($r = -0.79$, $p < 0.05$) correlated positively and negatively, respectively, with water level fluctuations (Figure 6.5.). Only TDP and K^+ exhibited a significant correlation with water level in the bog. As the water level dropped, TDP surface water concentrations increased and K^+ concentrations decreased. Potassium may be the growth limiting nutrient in this ombrotrophic site aside from water. Potassium plays an important role in plant production. It is a mineral necessary for enzymatic activities during photosynthesis and respiration as well as starch and protein formation in plant cells (Salisbury & Ross, 1985).

The effects of water level and climatic variables on plant tissue nutrient concentrations

Carex lasiocarpa in the lacustrine sedge fen

Nitrogen tissue concentrations in late June ranged from 1.90% (1994) to 1.76% (1993), and decreased towards the end of each growing season (Table 6.5.). Generally, late June tissue C:N ratios did not vary significantly among years, although they did increase significantly throughout the 1992 and 1994 growing seasons ($p < 0.05$) (Table 6.5.).

June total phosphorus tissue concentrations ranged from 1,411.5 µg/g dry weight in 1992 (0.14%) to 1,902.8 µg/g dry weight in 1994 (0.19%) and decreased towards the end of each growing season (Table 6.6.).

Carex lasiocarpa tissue N and TP concentrations correlated best with GDD ($r = -0.92$, $p < 0.001$, and $r = -0.69$, $p < 0.05$, respectively) (Table 6.2.). Also, adjusted conductivity ($r= 0.52$, $p < 0.05$), NH_4^+ ($r = 0.43$, $p < 0.05$) and air temperature ($r = -0.24$, $p < 0.05$) correlated significantly with tissue TP concentrations in *C. lasiocarpa* from the LSF (Table 6.2.). However, these correlations were substantially weaker than that of GDD. No significant correlation between water level and tissue nutrient concentrations was found in the LSF from 1991 to 1994 ($p > 0.05$) (Table 6.2.).

The number of growing degree days proved to be the variavble most closely related to tissue nutrient concentrations in *Carex lasiocarpa*. As the number of growing degree days increased, tissue nutrient concentrations decreased. Growing degree days were correlated with air temperature, and GDD in June, July and August were significantly higher than in May from 1991 to 1994 ($p < 0.0001$). The relationship between GDD and tissue nutrient concentrations has to be examined with caution though, as both sedges are perennials and translocate nutrients from aboveground to belowground tissues as the fall approaches. These nutrients are stored as energy reserves to be used for growth in the following spring. Other factors, such as hours of daylight or soil temperature, may be just as or more important in determining the onset and rate of nutrient translocation in these perennials.

Decreases in tissue nutrient concentrations during the latter part of the growing season can also be attributed to dilution and metabolism of nutrients in plants due to increasing rates of production, and leaching from aboveground tissues in addition to translocation into belowground tissues. These processes have been measured in *Carex lyngbyei* from a tidal marsh in the Fraser River estuary, British Columbia (Kistritz et al., 1983).

Vermeer & Verhoeven (1987) found that the amount of rain and groundwater input into fens in the Netherlands affected the levels of nutrients and minerals in plant tissues. As flow rates of water and amounts of precipitation increased, so did tissue N concentrations. They also determined that N levels in precipitation were very high due to the heavy industrialization of western Europe and that their ecosystems received substantial amounts of nitrogen from precipitation in addition to that from groundwater flow. Chapin III et al. (1988) measured plant production in the Alaskan tundra and found that water flow greatly enhanced plant growth in a water track compared to a non-water track. They attributed this, in part, to higher ground temperatures, which lead to greater rates of litter decomposition and nutrient mineralization. Auclair (1977) found a positive relationship between water depth and tissue element concentrations in wet meadow vegetation. Flooding exposed plants to higher concentrations of nutrients, which resulted in higher rates of nutrient uptake by wet meadow species, such as several *Carex* spp..

If the water table level drops in response to higher atmospheric temperatures, I speculate that tissue nutrient concentrations of N and TP in *Carex lasiocarpa* will not change substantially. Mean annual water levels were significantly different among years, yet they did not correlate significantly with tissue N and TP concentrations in this sedge.

Eriophorum vaginatum in the bog

Late August tissue nitrogen concentrations ranged from 1.31% (1991) to 2.13% (1994) (Table 6.5.). Due to the variability in %N tissue concentrations, C:N ratios were highly variable as well. The C:N ratios increased in 1991 and decreased in 1994 towards the end of the growing season (Table 6.5.).

Total phosphorus (TP) tissue concentrations in *Eriophorum vaginatum* generally decreased towards the end of the growing season (Table 6.6.); however, it was difficult to detect any clear trends from 1991 to 1994.

Tissue nutrient concentrations of nitrogen (N) and total phosphorus (TP) in *Eriophorum vaginatum* from the bog correlated best with NH_4^+ ($r = -0.81$, $p < 0.05$) and the number of growing degree days (GDD) ($r = -0.67$, $p < 0.05$), respectively (Table 6.2.).

The close relationship between tissue TP concentrations and GDD in *Eriophorum vaginatum* has to be taken with caution for the same reasons previously discussed and the alternative mechanisms which may be responsible for tissue nutrient concentration decreases. The negative correlation between tissue N concentrations and NH_4^+ ($r = -0.81$, $p < 0.05$) in *E. vaginatum* in the bog may be attributed to the previously discussed inhibitory effect of ammonium. Therefore, nutrient concentrations in aboveground tissues may be negatively affected as well.

Loach (1967) found that drainage generally increased tissue nutrient concentrations of N and P in *Molinia* sp. in a valley bog in Hampshire, England. However, he also determined that if a peatland is nutrient-poor, drainage will not result in any substantial changes in nutrient and mineral concentrations in plant tissues. Our data suggests that NH_4^+ concentrations in the surface water negatively affect tissue N concentrations in *Eriophorum vaginatum*. Since the water level did not fluctuate significantly among years in the bog, it did not prove to be a significant factor in affecting tissue nutrient concentrations. However, K^+ surface water concentrations exhibited a significant negative correlation with the position of the water level relative to the peat surface and low concentrations of this ion may compound the toxicity effects of NH_4^+. Therefore, a lowered water table may indirectly cause decreased tissue N concentrations in *E. vaginatum*.

The effects of climate on plant production

Lacustrine sedge fen

Air temperature was the only climatic variable which exhibited a significant correlation with herb production in the LSF ($r = 0.32$, $p < 0.05$) (Table 6.2.). Shrub and moss NPP did not correlate with any climatic factor in the fen ($p > 0.05$).

Gorham (1974) previously demonstrated that summer air temperature correlated significantly with *Carex* spp. production in eight North American and northern European wetlands between 42° to 68° N latitude ($r = 0.84$, $p < 0.01$). Also, Gorham's (1974) correlation is substantially stronger than mine ($r = 0.32$), which, I speculate, is the result of the prominent role water level fluctuations played on herb production in the LSF ($r = 0.73$). Furthermore, water level fluctuations significantly affected the concentration of some surface water chemistry parameters, which could have further diminished the influence of growing season air temperature on herb production.

The number of growing degree days (GDD) (Droste, 1984; Gorham, 1974) and latitude (Bernard & Gorham, 1978) have also been found to significantly affect herb growth in North American wetlands. Latitude was not a factor in this study and total growing season GDD were not significantly different from 1991 to 1994 ($p > 0.05$).

If climatic warming causes a drop in the water level, the results of this study suggest that shrub production will increase and herb production will decrease in this fen. The four year correlation between water level and shrub production was weak and contradicts previous findings for Alberta peatlands (Chapter four; Szumigalski & Bayley, under review (c)). Also, shrubs grew almost exclusively on drier hummocks. Water availability and decreased calcium concentrations in the surface water will reduce herb growth, whereas deeper rooted shrubs will have greater access to nutrients and water. The response of mosses in this fen can not be predicted from my data. *Drepanocladus aduncus*, a hollow species, may also be limited by nutrients and water and I speculate that production of this drought-intolerant species will decrease as well. Therefore, the vegetation composition of this lacustrine sedge fen will change under a warmer climate if the water level drops.

Gorham (1990) described the succession from sedge-dominated fens to poor fens to bogs. It is possible that this lacustrine sedge fen may undergo a similar succession under a drier, warmer climate. Shrubs may become the dominant vegetation by replacing herbs, and *Sphagnum* spp. may replace the presently dominant "brown" moss species. This fen might gradually convert into a poor fen and, if the basin is large and moist enough, ultimately into a bog (Gorham, 1990), dominated by *Picea mariana* and *Sphagnum* spp. (Glaser & Janssens, 1986).

Bog

Production of *Sphagnum fuscum* and shrubs correlated significantly with air temperature ($r = 0.84$, $p < 0.01$) and GDD ($r = 0.52$, $p < 0.01$), respectively (Table 6.2.). No other climatic variables correlated significantly with plant production in the bog.

A strong correlation between *Sphagnum* spp. production and temperature has previously been reported by Moore (1989) in five poor to moderate-rich fens in Quebec, Canada. His correlation was substantially weaker than mine ($r = 0.55$ versus $r = 0.84$) and may be the result of the variation of the peatlands he examined, whereas mine refers to the same bog over four years.

Other studies found significant correlations between moss growth and timing of precipitation (Backéus, 1988) and position of the water table with respect to the peat surface (Brock & Bregman, 1989; Backéus, 1988; Wieder & Lang, 1983). Neither of these two parameters were significiant in this study as the mean annual water level and timing and total amounts of precipitation did not vary significantly from 1991 to 1994 (both $p > 0.05$).

Shrub production was found to correlate significantly with GDD in the bog. The effects of climatic variables on shrub growth are very scarce and most often water level fluctuations (Chapter four; Szumigalski & Bayley, under review (c); Gorham, 1991; Hillman et al., 1990; Moore, 1989; Vasander, 1982) and surface water chemistry parameters affect shrub production to a greater extent and possibly mask the effects of climatic variables.

Shrub production did not vary significantly among years ($p > 0.05$) in the bog. The non-significant increase in shrub production from 1991 to 1994 can be attributed to the increasing concentrations of soluble reactive phosphorus (SRP) in the surface water (Table 6.3.); the correlation between these two variables was strong ($r = 0.84$, $p < 0.05$) (Table 6.2.) and the age of the plants.

The mean annual water level did not vary significantly among years and did not affect moss, herb or shrub production directly. The effects of NH_4^+ and low K^+ surface water concentrations on herb production and tissue N concentrations were discussed earlier and ammonium toxicity in mosses has also been reported previously (Chapter five; Vasander, 1982). Shrub and moss production correlated significantly with GDD and air temperature, thus, increased atmospheric temperatures may lead to increased production of these two strata. Furthermore, a lowered water level resulting from increased production and warmer air temperatures may also lead to increased production of shrubs and trees. This relationship has been demonstrated in a Finnish bog (Vasander, 1982) and an Alberta bog (Hillman et al., 1990). In addition, Pakarinen (1978) determined that leaching rates of nutrients and minerals, especially K^+, from surface to deeper peat layers are enhanced in bogs with a lowered water table. This may further compound the potential NH_4^+ toxicity on herb species and reduce their productivity. Therefore, I speculate that it is possible that the vegetation composition of this bog may change in response to a warmer and drier climate, moss and herb production may decline and deeper rooted shrubs and trees may become the dominant vegetation strata by retaining their access to water, nutrients and minerals. Fires may become more frequent and burn off peat layers (Flannigan & Van Wagner, 1991), possibly leading to the disappearance of peat from this site.

Conclusions

The net primary production (NPP) of the moss, herb and shrub strata, surface water chemistry parameters and water level fluctuations were measured in a bog and a lacustrine sedge fen (LSF) from 1991 to 1994. Based on the data collected by Szumigalski & Bayley (under review, (a), (b), (c)) and myself, inferences for global warming were made regarding these parameters in the two peatlands.

The mean annual water level and NO_3^- surface water concentrations correlated best with herb and shrub production in the LSF ($r = 0.73$ and $r = 0.86$, respectively). Air temperature, NH_4^+ and SRP showed the strongest correlation with moss ($r = 0.84$), herb ($r = -0.81$) and shrub ($r = 0.84$) production in the bog. Tissue nutrient concentrations of N and TP in *Carex lasiocarpa* in the LSF exhibited the best correlation with GDD ($r = -0.67$) and NH_4^+ concentrations in the surface water ($r = -0.81$), respectively. In the bog, GDD correlated best with both N ($r = -0.92$) and TP ($r = -0.69$) tissue concentrations in *Eriophorum vaginatum*.

Mean annual water levels varied significantly among years in the LSF and positive and negative correlations between water level and Ca^{2+} ($r = 0.75$) and NO_3^- ($r = -0.45$) surface water concentrations were evident. In the bog, mean annual water levels did not vary significantly among years; however, K^+ ($r = 0.94$) and TDP ($r = -0.79$) surface water concentrations correlated significantly with the water level relative to the peat surface from 1991 to 1994.

I speculate that a warmer and drier climate may lead to a succession from the lacustrine sedge fen to a poor fen and ultimately to a bog. Herbs and "brown" mosses may be displaced by shrubs and trees or replaced with *Sphagnum* spp., respectively. The bog may succeed into an upland-type forest ecosystem, where shrubs and trees dominate and mosses do not contribute significantly to the total production of the ecosystem. Increased fire occurences may burn off the peat in both sites.

Vance et al. (1995) showed that between 6,000 and 9,000 years ago, the southern boreal forest regions in Alberta experienced summer temperatures between 0.5 and 3.0 °C higher than present. As a result, the water table dropped, which led to a northward migration of grasslands. Pollen diagrams from Lofty Lake (approximately 150 km north east of Edmonton) showed that woody plant species, such as *Salix* spp. and *Populus* spp., and Gramineae (grasses) exhibited a greater abundance during that period than during the cooler and moister period thereafter until the present (Lichti-Federovich, 1970). Furthermore, basal dates from peatlands in western Canada suggest that the water table was also lower in peatlands, which inhibited moss growth in fens (Zoltai & Vitt, 1990).

Therefore, bogs and fens in Alberta with a similar vegetation composition and surface water chemistry may undergo successional changes as well under a warmer, drier climate if the water level drops as anticipated. Based on these results, sedge-dominated fens will experience these changes before shrub- and tree-dominated bogs due to the different environmental requirements of the dominant vegetation strata in these two types of peatlands.

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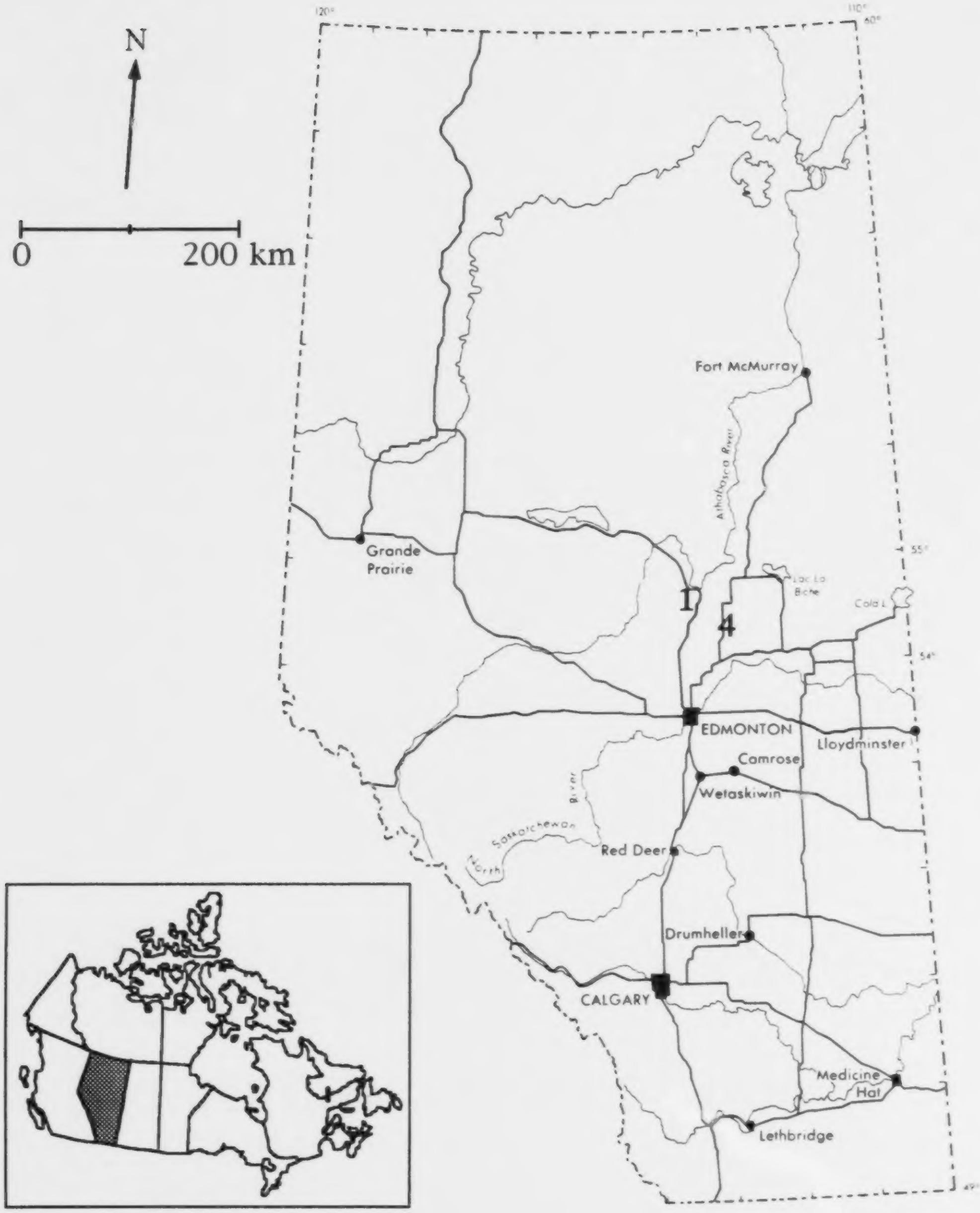
N
0
200 km
120°
110°
60°
55°
54°
49°
Fort McMurray
Athabasca River
Grande Prairie
Lac La Biche
Cold L.
1
4
EDMONTON
Lloydminster
Camrose
Wetaskiwin
North Saskatchewan River
Red Deer
Drumheller
CALGARY
Medicine Hat
Lethbridge

Figure 6.1. Relative location of the two peatlands in central Alberta (**1** = bog, **4** = lacustrine sedge fen). These two sites represent part of a larger group of peatlands currently under investigation.

Table 6.1. Climatic data for May - August 1991 to 1994 and long term (1951-1980) averages from the Athabasca 2 weather station. Growing degree days (GDD) is measured as the sum of daily mean temperatures > 5 °C.

Athabasca 2 weather station		**May**	**June**	**July**	**August**	**May - August Mean / Total**
1991						
	Mean temp. (°C)	11.5	13.8	16.8	18.3	15.1
	GDD	203.3	265.0	366.7	412.6	1247.6
	Precip. (mm)	60.4	100.2	54.2	43.4	258.2
	Precip. days	11	17	14	9	51
1992						
	Mean temp. (°C)	9.6	15.1	15.1	14.3	13.5
	GDD	153.9	302.9	314.0	290.1	1060.9
	Precip. (mm)	50.2	55.2	84.0	45.6	235.0
	Precip. days	11	12	16	8	47
1993						
	Mean temp. (°C)	11.4	13.4	14.9	14.7	13.6
	GDD	198.0	251.9	306.1	300.2	1056.2
	Precip. (mm)	39.2	73.4	237.4	83.8	433.8
	Precip. days	6	12	21	13	52
1994						
	Mean temp. (°C)	10.9	14.1	16.7	15.7	14.4
	GDD	197.0	271.4	361.6	331.1	1161.1
	Precip. (mm)	65.4	110.2	116.2	30.6	322.4
	Precip. days	11	15	17	6	49
Long term average						
	Mean temp. (°C)	10.1	14.1	16.2	14.8	13.8
	Precip. (mm)	44.9	80.1	90.0	68.2	283.2

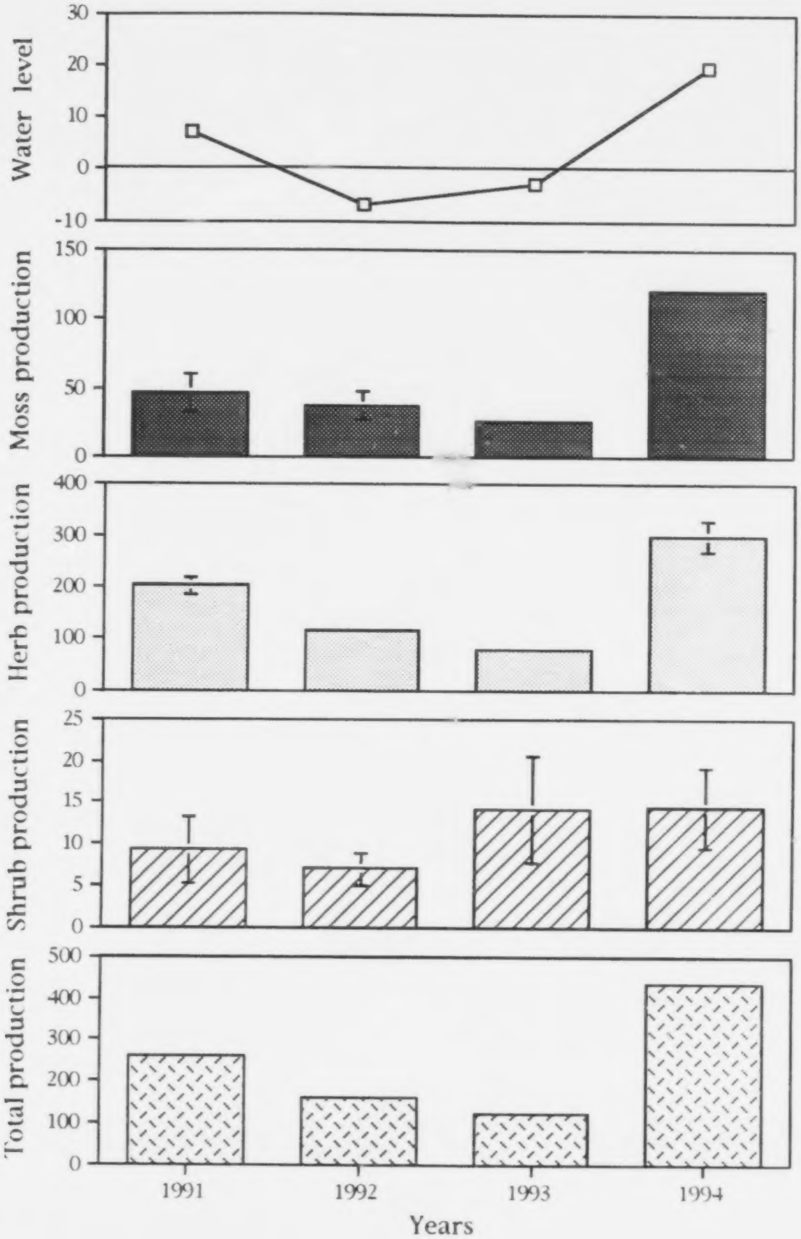

Figure 6.2. Mean (+/- SE) peak vascular and non-vascular plant production and total plant production (g/m^2/year) in the lacustrine sedge fen (LSF) from 1991 to 1994 in relation to the water level (relative to the peat surface, 0 cm). Error bars absent where SE < 10 g/m^2/year (columns) and SE < 1.5 cm (symbols) (mean annual water levels). Note the different scales on the y-axes.

Table 6.2. Correlation coefficients of moss, herb and shrub production and tissue total phosphorus (TP) and nitrogen (N) content of the dominant herb species with surface water chemistry and climatic parameters in the bog and the lacustrine sedge fen (LSF) from 1991 to 1994.

	Bog		**LSF**	
	Parameter	**r**	**Parameter**	**r**
Moss production	Temperature	0.84 **	Not determined due to small sample size (n=3)	
Herb production	NH4+	-0.81 *	Water level	0.73 ***
			Temperature	0.32 *
Shrub production	SRP	0.84 *	NO3-	0.86 *
	GDD	0.52 **	TP	-0.47 *
			Water level	0.22 **
Tissue nutrient content				
	Eriophorum vaginatum		***Carex lasiocarpa***	
TP	GDD	-0.67 *	GDD	-0.69 *
			Adjusted conductivity	0.52 *
			NH4+	0.43 *
			Temperature	-0.24 *
N	NH4+	-0.81 *	GDD	-0.92 ***
	TP	0.49 *		

* $p < 0.05$	GDD = Growing degree days
** $p < 0.01$	SRP = Soluble reactive phosphorus
*** $p < 0.001$	TP = Total phosphorus

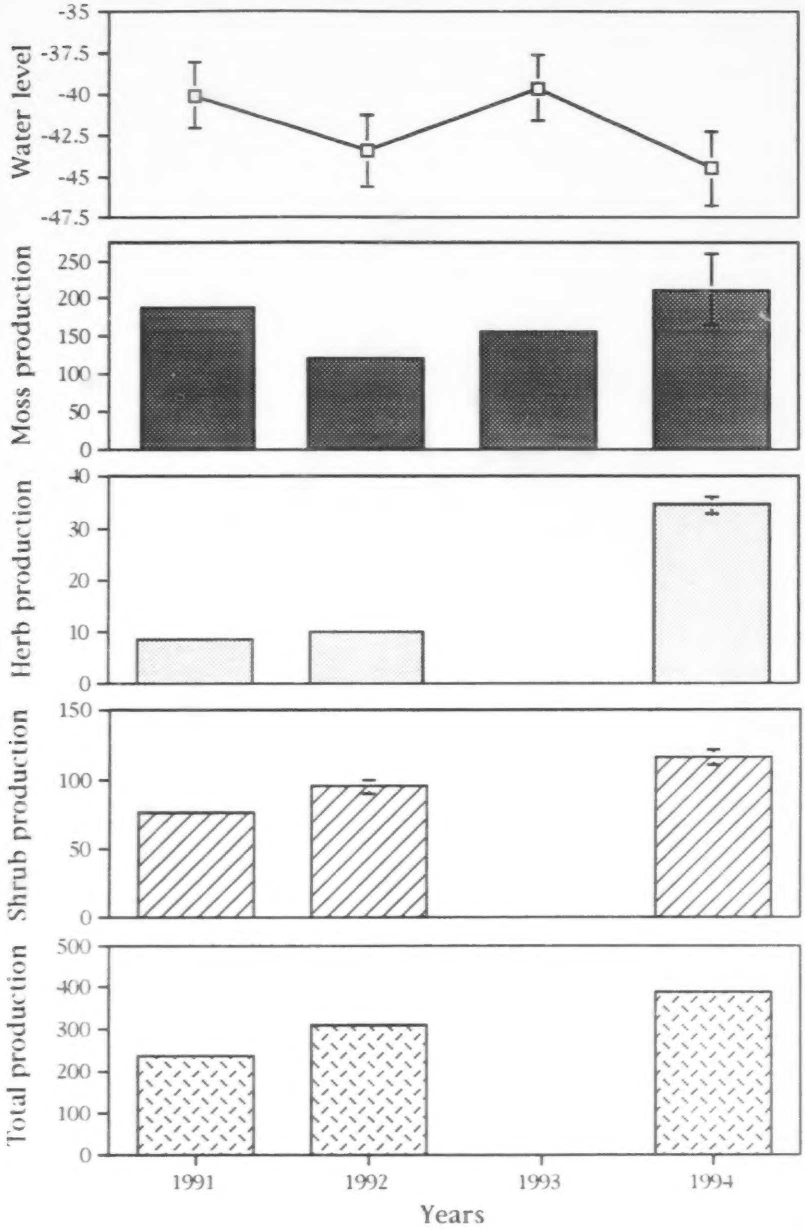

Figure 6.3. Mean (+/- SE) peak vascular and non-vascular plant production and total plant production (g/m^2/year) in the bog from 1991 to 1994 in relation to the water level (relative to the peat surface, 0 cm). Vascular and total plant production was not measured in 1993. Error bars absent where SE < 8 g/m^2/year. Note the different scales on the y-axes.

Table 6.3. Annual means (ranges) of surface water chemistry parameters in the bog from 1991 to 1994.

Characteristic	**1991**	**1992**	**1993**	**1994**
Water table depth (cm)	-40.0 (-33.3 - -45.6)	-43.4 (-35.8 - -51.8)	-39.6 (-28.1 - -49.8)	-44.5 (-32.9 - -51.2)
Depth of oxidation (cm)	-- --	30.5 (19.2 - 43.3)	20.8 (9.6 - 31.0)	27.5 (22.3 - 30.4)
pH	3.73 (3.39 - 3.91)	3.98 (3.86 - 4.22)	4.20 (3.64 - 3.94)	3.60 (3.38 - 4.12)
Adjusted conductivity (μS)	0.0 --	0.0 --	0.0 --	0.0 --
Alkalinity (mg/L CaCO3)	0.0 --	0.0 --	0.0 --	0.0 --
HCO3- (mg/L)	0.0 --	0.0 --	0.0 --	0.0 --
NO3- (μg/L)	10.9 (6.0 - 24.4)	6.9 (2.7 - 15.1)	7.8 (2.0 - 16.6)	6.0 (3.2 - 12.6)
NH4+ (μg/L)	40.2 (25.1 - 47.7)	43.4 (12.2 - 107.5)	50.3 (b. d. - 202.0)	29.4 (b. d. - 52.9)
SRP (μg/L)	8.2 (2.6 - 19.3)	23.8 (1.4 - 63.3)	9.0 (2.7 - 26.4)	31.2 (2.5 - 75.4)
TDP (μg/L)	44.8 (21.4 - 84.2)	68.0 (32.4 - 152.9)	37.9 (23.3 - 89.6)	79.1 (34.0 - 132.3)
TP (μg/L)	147.6 (34.3 - 248.8)	158.7 (46.0 - 386.8)	72.9 (36.6 - 128.4)	147.3 (58.9 - 297.3)
K+ (mg/L)	0.9 (0.61 - 1.22)	0.9 (0.32 - 1.42)	1.2 (0 - 1.96)	1.9 (1.59 - 2.79)
Na+ (mg/L)	1.5 (1.33 - 1.69)	2.1 (1.86 - 2.25)	1.7 (1.20 - 2.20)	1.0 (0.78 - 1.25)
Ca2+ (mg/L)	3.1 (2.26 - 4.56)	4.9 (4.25 - 5.46)	4.0 (0 - 19.80)	2.1 (1.23 - 2.79)
Mg2+ (mg/L)	1.0 (0.78 - 1.25)	1.8 (1.12 - 2.40)	1.6 (0 - 7.80)	0.9 (0.55 - 1.14)
Cl- (mg/L)	0.7 (0.54 - 0.78)	0.5 (0.21 - 1.08)	0.9 (0.08 - 2.49)	0.6 (0.37 - 0.74)
Sulfate (mg/L)	1.2 (1.00 - 1.48)	0.8 (b. d. - 1.36)	0.7 (b. d. - 2.27)	0.4 (0 - 0.69)

SRP = soluble reactive phosphorus
TDP = total dissolved phosphorus
TP = total phosphorus
b. d. = below detection

Table 6.4. Annual means (ranges) of surface water chemistry parameters in the lacustrine sedge fen (LSF) from 1991 to 1994.

Characteristic	**1991**	**1992**	**1993**	**1994**
Water table depth (cm)	7.09 (-7.6 - 19.8)	-6.79 (-16.4 - 1.7)	-2.80 (-12.7 - 4.7)	19.60 (6.4 - 27.5)
Depth of oxidation (cm)	-- --	16.4 (0.50 - 31.0)	8.2 (5.5 - 10.0)	3.9 (2.43 - 5.73)
pH	6.60 (6.26 - 6.85)	6.43 (6.42 - 7.51)	6.95 (6.20 - 7.77)	7.01 (6.52 - 7.40)
Adjusted conductivity (μS)	71.4 (55.8 - 79.2)	41.0 (30.0 - 51.4)	108.7 (94.0 - 132.0)	180.7 (57.0 - 286.0)
Alkalinity (mg/L CaCO3)	-- --	61.0 (52.7 - 74.1)	50.3 (19.5 - 63.5)	100.1 (74.1 - 136.3)
HCO3- (mg/L)	-- --	74.4 (64.8 - 90.3)	61.3 (23.8 - 77.5)	122.0 (90.4 - 166.1)
NO3- (μg/L)	7.9 (3.6 - 14.7)	6.2 (3.1 - 10.8)	7.9 (3.4 - 20.7)	2.6 (b. d. - 7.6)
NH4+ (μg/L)	17.7 (9.1 - 26.2)	23.7 (1.9 - 67.5)	41.6 (b. d. - 64.1)	11.4 (b. d. - 90.2)
SRP (μg/L)	4.5 (0.8 - 10.8)	6.6 (1.6 - 16.5)	4.3 (0.8 - 13.6)	4.5 (1.8 - 10.7)
TDP (μg/L)	19.0 (10.0 - 30.0)	27.4 (13.2 - 39.5)	20.3 (9.9 - 46.0)	18.4 (9.3 - 30.7)
TP (μg/L)	94.0 (15.1 - 263.1)	146.8 (40.3 - 266.9)	53.2 (21.1 - 88.6)	60.9 (13.0 - 196.9)
K+ (mg/L)	1.2 (0.27 - 2.31)	1.1 (0.45 - 1.72)	1.8 (0.32 - 3.00)	1.6 (0.28 - 2.98)
Na+ (mg/L)	5.0 (3.31 - 5.57)	4.2 (2.81 - 5.58)	4.7 (1.72 - 4.67)	5.0 (4.75 - 7.42)
Ca2+ (mg/L)	22.6 (7.2 - 35.8)	14.1 (10.8 - 17.4)	18.6 (7.2 - 50.5)	24.2 (18.7 - 37.0)
Mg2+ (mg/L)	8.5 (7.2 - 12.2)	4.8 (2.3 - 7.2)	8.1 (2.6 - 25.6)	8.7 (7.6 - 13.1)
Cl- (mg/L)	1.1 (0.70 - 1.40)	0.5 (0.16 - 0.83)	0.4 (b. d. - 0.98))	0.5 (0.37 - 0.73)
Sulfate (mg/L)	> 0.5 (b. d. - 0.5)	b. d. --	b. d. --	b. d. --

SRP = soluble reactive phosphorus
TDP = total dissolved phosphorus
TP = total phosphorus
b. d. = below detection

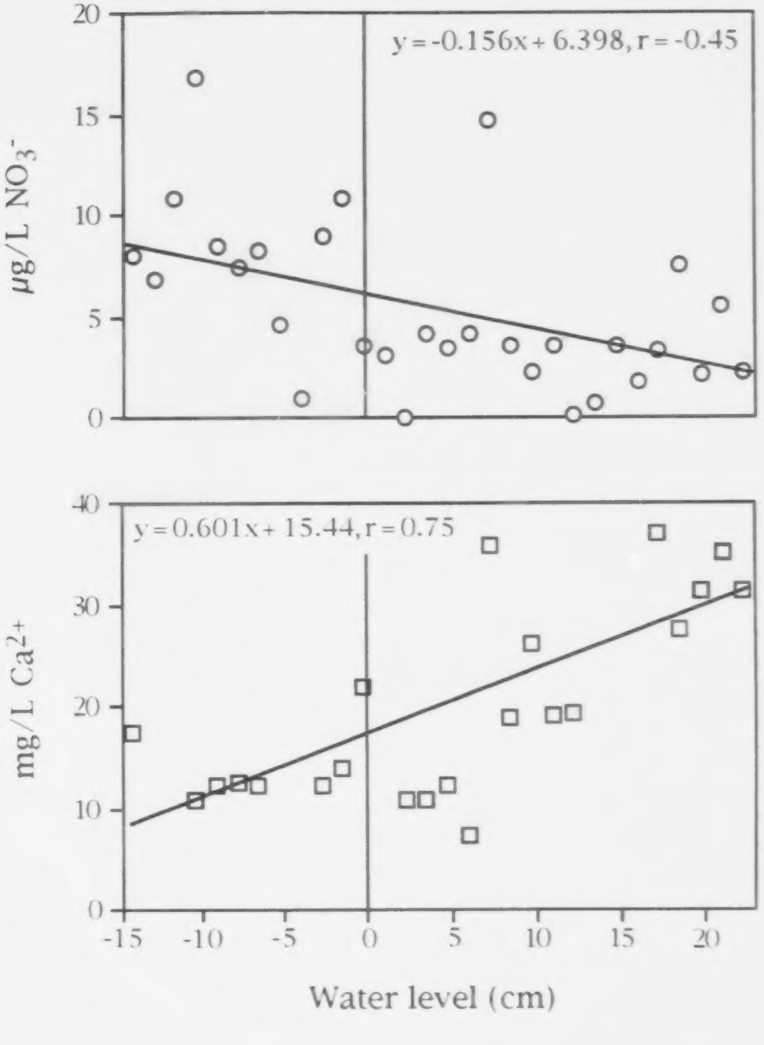

Figure 6.4. Nitrate (NO_3^-, μg/L) and calcium ion (Ca^{2+}, mg/L) surface water concentrations in relation to the water level relative to the peat surface (0 cm) in the lacustrine sedge fen (LSF) from 1991 to 1994.

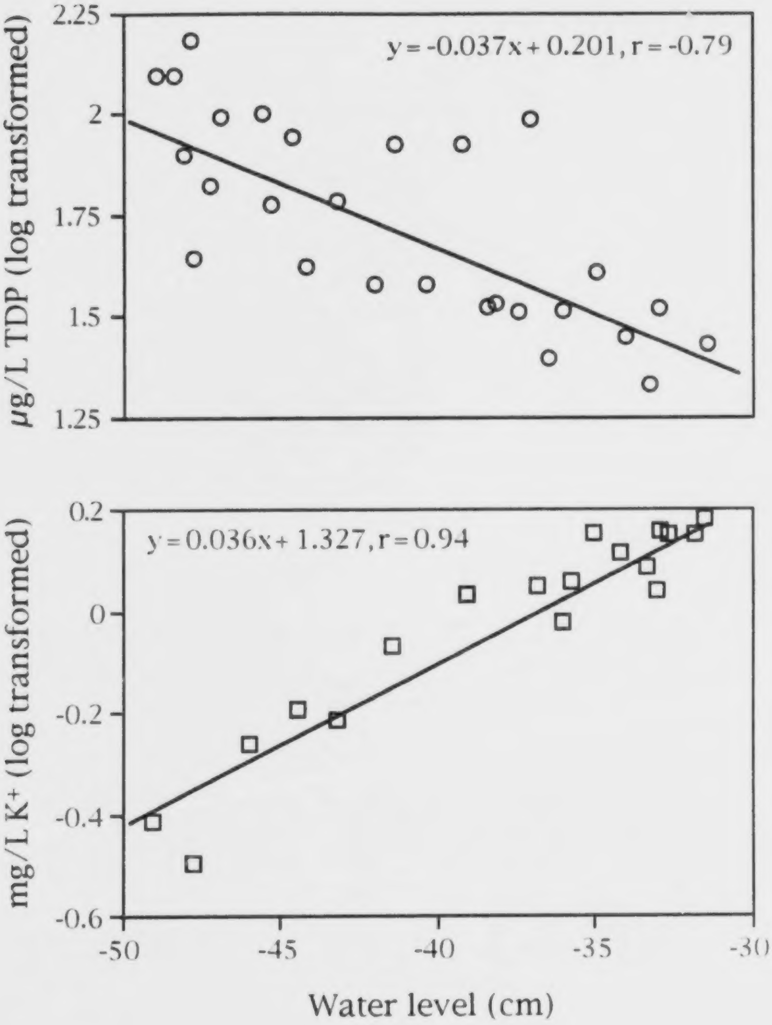

Figure 6.5. Total dissolved phosphorus (TDP, μg/L, log transformed) and potassium ion (K^+, mg/L, log transformed) surface water concentrations in relation to the water level relative to the peat surface (0 cm) in the bog from 1991 to 1994.

Table 6.5. Mean (+/- SE) percent nitrogen and C:N ratios of two herb species in two peatlands (bog, LSF = lacustrine sedge fen) from 1991 to 1994 (neither site was measured in June, 1991; the bog was not measured in 1993).

		1991						1992					
Site	Species	June 26 %N	July 26 %N	Aug. 26 %N	June 26 C:N	July 26 C:N	Aug. 26 C:N	June 26 %N	July 26 %N	Aug. 26 %N	June 26 C:N	July 26 C:N	Aug. 26 C:N
Bog	*Eriophorum*	--	1.53	1.31	--	30.84	35.47	1.62	1.39	1.71	28.88	33.61	26.87
	vaginatum	--	(0.15)	(0.03)	--	(2.88)	(1.01)	(0.13)	(0.16)	-- *	(2.52)	(3.20)	-- *
LSF	*Carex*	--	1.64	1.52	--	27.3	29.67	1.84	1.67	1.29	23.99	26.56	36.57
	lasiocarpa	--	(0.01)	(0.02)	--	(0.26)	(0.42)	(0.01)	(0.06)	(0.17)	(0.01)	(0.85)	(5.89)

		1993						1994					
Site	Species	June 26 %N	July 26 %N	Aug. 26 %N	June 26 C:N	July 26 C:N	Aug. 26 C:N	June 26 %N	July 26 %N	Aug. 26 %N	June 26 C:N	July 26 C:N	Aug. 26 C:N
Bog	*Eriophorum*	--	--	--	--	--	--	1.75	1.90	2.13	25.17	24.47	22.21
	vaginatum	--	--	--	--	--	--	(0.06)	(0.05)	(0.14)	(0.63)	(0.60)	(1.60)
LSF	*Carex*	1.76	1.60	1.54	25.62	28.22	29.24	1.90	1.47	1.30	23.8	30.94	35.15
	lasiocarpa	(0.07)	(0.08)	(0.04)	(1.07)	(1.33)	(0.80)	(0.08)	(0.08)	(0.06)	(1.32)	(1.60)	(1.68)

* = not determined due to small sample size (n=1)

Table 6.6. TP (total phosphorus, ug/g) content of two species in two peatlands (bog, LSF = lacustrine sedge fen) from 1991 to 1994 (neither site was measured in June, 1991; the bog was not measured in 1993).

		1991			1992			1993			1994		
Site	**Species**	**June**	**July**	**August**	**June**	**July**	**August**	**June**	**July**	**August**	**June**	**July**	**August**
Bog	*Eriophorum vaginatum*	--	1,334.3	1,054.9	1,541.3	1,147.7	1,348.2	--	--	--	1,537.9	1,697.8	1,178.9
LSF	*Carex lasiocarpa*	--	1,404.2	1,121.6	1,411.5	1,299.9	1,135.6	1,566.6	1,364.2	1,349.2	1,902.8	1,424.7	1,323.6

7. CONCLUSIONS

Plant production (NPP), decomposition, surface water chemistry parameters, water level fluctuations and plant tissue nutrient concentrations of the dominant plant species were measured in five sites in 1993 and 1994 and in an addition sixth site in 1994. These sites are representatives of a bog - moderate- to rich fen - eutrophic marsh peatland gradient in southern boreal Alberta, Canada. The sites were a bog, a lacustrine sedge fen (LSF), an open rich fen (ORF), a riverine sedge fen (RSF), a riverine marsh (RM) and a lacustrine marsh (LM).

I hypothesized that an increasing gradient of plant production from bogs to fens to marshes exists and this hypothesis was partially proven (Chapter two). Total NPP of the bog was 390 g/m^2/year, the fens averaged 277 to 409 g/m^2/year and the marshes averaged 323 to 757 g/m^2/year. Bog and fen NPP were similar but significantly less than that of the marshes. Moss production was more variable between years than among sites and appeared to be correlated with climatic variables. Moss NPP decreased along the peatland gradient and were negligible or absent in the RSF, RM and LM. Herb production varied significantly between years and among sites within years and increased along the peatland gradient. A strong correlation with the position of the water level relative to the peat surface was found ($r = 0.73$). Herb production ranged from 35 g/m^2/year in the bog to averages of 252 g/m^2/year in the fens and 551 g/m^2/year in the marshes during 1993 and 1994. Shrub production varied significantly among sites but not between years within sites. Production values ranged from a maximum of 126 g/m^2/year (bog) to 14 g/m^2/year (LSF) in those sites with a shrub stratum. Shrubs were absent in the RSF, RM and LM, possibly due to the consistently high water levels in these sites ($r = -0.74$).

Soluble reactive phosphorus (SRP) appeared to be the single most important factor in affecting vascular and total plant production in fens and marshes in 1993 and 1994 (Chapter four). Total phosphorus (TP), alkalinity and NO_3^- were also important surface water parameters.

The bog and fen NPP values were intermediate for North American wetlands and conformed to a latitudinal NPP gradient. The marshes of this study were substantially less productive than most marshes in Canada at similar latitudes, indicating the importance of the species composition in affecting NPP. Net primary plant production was higher in most sites in 1993 than in 1994, except for the RM, whose water supply was blocked off by beaver dams during the second year of this study.

Fertilization with N or P at a 7:1 loading rate ratio could not answer the question of which nutrient limits plant production in Alberta peatlands (Chapter five). There were no significant increases in total plant production in either the fens or marshes. Ericaceous and deciduous shrubs, herbs and mosses responded variably to the addition of N, P or water in the bog. Ericaceous shrubs showed positive and negative responses to fertilization. Herb NPP generally increased with fertilization and deciduous shrubs showed no response. Moss production increased significantly after the addition of water but not with N or P dissolved in water. Therefore, predicting species specific responses was unsuccessful and did not support the hypothesis that a plant's life form determines how it will respond to a nutrient perturbation. Fungal and microbial uptake immediately following the application of fertilizer and/or luxury consumption by the vegetation strata may explain these results.

Differences in weight losses of the dominant and standard plant litters and cellulose (filterpaper) were partially explained by differences in litter quality and environmental differences among sites (Chapter three). *Carex lasiocarpa*, native to all minerotrophic sites, lost between 45.2 (RSF) and 68.5% (LSF) in fens and between 58.1 (RM) and 72.3% (LM) in marshes over 456 days starting in 1993. Weight losses were significantly different among individual sites but not between fens and marshes (once combined into peatland "types").

Cellulose decayed significantly faster in the eutrophic marshes (mean of 66.9%) than in the oligotrophic fens (mean of 28.2%) over 100 days in 1994. *Carex aquatilis* from the RSF decomposed at a similar rate in fens and marshes over 100 days in 1994. Leaching of soluble organic materials from *C. aquatilis* accounted for an initial weight loss of 6.80% over 7 days *in vitro*. This represented the amount of organic compounds which leaches out of plant litter during the first phase of decomposition and had to be accounted for since the plant litter of these experiments were quantitatively richer in nutrients than plant litter decomposing in the fall *in situ*.

NH_4^+ concentrations in the surface water related best to plant litter decay (*Carex lasiocarpa* and *Carex aquatilis*), whereas SRP concentrations in the surface water best explained weight losses of cellulose in fens. Decomposition of *C. lasiocarpa* (dominant plant species) was best related to water levels relative to the peat surface. SRP concentrations in the surface water best explained weight losses of *C. aquatilis* (standard plant litter) and cellulose in marshes.

The C:N ratios of decaying *Carex aquatilis* generally decreased in the marshes but increased in the fens over 100 days in 1994. %N tissue concentrations exhibited the reverse trends and %C levels generally remained unchanged over this period. There were no clear trends detected in the C:N ratio and %N tissue concentrations for the dominant plant litter, *Carex lasiocarpa*.

Chapters four & six summarize changes of %C, %N, C:N and TP tissue concentrations in *Carex lasiocarpa* (from all fens and marshes) and *Eriophorum vaginatum* (from the bog) from late June to late August. Tissue nutrient concentrations in *C. lasiocarpa* exhibited similar trends in the fens and marshes with N and TP content decreasing, %C remaining similar and the C:N ratios increasing during this period. *Eriophorum vaginatum* tissue concentrations of N and TP showed variable response patterns; however, %C levels remained similar.

Four years of measurements of NPP, surface water chemistry and water level fluctuations from the LSF and the bog were used to make inferences regarding the future status of similar peatlands in southern boreal Alberta due to lowered water levels in response to global climate warming (Chapter six). The data was collected (1991 to 1994) as part of my studies and those of Szumigalski (M.Sc. Thesis, 1995).

The position of the water level relative to the peat surface and some climatic variables, such as air temperature and growing degree days, correlated significantly with moss, herb and shrub production and tissue nutrient concentrations in the bog and the LSF. Also, water level fluctuations significantly affected cation (positively) and nutrient (negatively) concentrations in both peatlands.

The results of this study suggest that if water levels drop in response to warmer and drier climatic conditions, the LSF will experience succession from a sedge-dominated fen to a poor fen and ultimately to a *Sphagnum* spp.- and *Picea mariana*-dominated bog. Shrubs and trees will dominate and herbs will contribute less to the total plant production. The bog may succeed into an upland-type forest ecosystem, where woody plant species dominate. The moss cover will contribute substantially less to the total plant production. In both sites, increased fire occurrences may burn off the peat layers.

Literature cited

Szumigalski, A.R., 1995. Production and decomposition of boreal wetlands. M.Sc. Thesis, Botany Department, University of Alberta, Edmonton. 117 pp.

Appendix 1: Climatic data for May - October 1993 and 1994 and long term (1951-1980) averages from the Athabasca 2 weather station. GDD is growing degree days measured as the sum of daily mean temperature > 5.0 °C.

Athabasca 2 weather station	**May**	**June**	**July**	**August**	**September**	**October**	**May - October Mean / Total**
1993							
Mean Temp. (°C)	11.4	13.4	14.9	14.7	9.8	4.4	11.4
GDD	198.0	251.9	306.1	300.2	144.9	148.6	1349.7
Precip. (mm)	39.2	73.4	237.4	83.8	33.0	29.2	496.0
1994							
Mean Temp. (°C)	10.9	14.1	16.7	15.7	12.4	4.7	12.4
GDD	197.0	271.4	361.6	331.1	224.0	30.8	1415.9
Precip. (mm)	65.4	110.2	116.2	30.6	43.2	21.2	386.8
Long term average							
Mean Temp. (°C)	10.1	14.1	16.2	14.8	9.5	4.6	11.6
Precip. (mm)	44.9	80.1	90.0	68.2	45.2	21.5	349.9

Appendix 2: Total aboveground plant production (g/m^2) of herbs and shrubs from five peatlands in 1993. Herb values are from the period of peak herb standing crop while the shrub values originate from the late August harvest period.

Plant type	**ORF**	**Riverine Sedge Fen**	**Lacustrine Sedge Fen**	**Riverine Marsh**	**Lacustrine Marsh**
Carex spp.	94.4	337.4	78.5	236.9	531.7
Potentilla palustris	7.2		1.7		
Menyanthes trifoliata	12.8				
Grasses (Agrostis, Scabra)	1.8				
Triglochin maritima	3.6				
Smilacina trifolia					
Rubus chamaemorus					
Eriophorum vaginatum					
Typha latifolia					46.1
Equisetum fluviatile		0.6			
Calamagrostis spp.				153.9	
Urtica dioica					
Mentha arvensis					
Galium trifidum				0.3	3.4
minor spp.	1.9	0.4	0.4	3	0.5
Salix spp.	11.7		14.2		
Andromeda polifolia	17.7				
Oxycoccus quadripetalus	3.6				
Ledum groenlandicum					
Vaccinium vitis-idaea					
Betula pumila					
Total production	**154.7**	**338.4**	**93.9**	**394.1**	**581.7**

Appendix 2: Total aboveground plant production (g/m^2) of herbs, shrubs and trees from six peatlands in 1994. Herb values are from the period of peak herb standing crop while the shrub values originate from the late August harvest period. Tree production was estimated from Szumigalski & Bayley (under review (a)).

Plant type	**Bog**	**ORF**	**Riverine Sedge Fen**	**Lacustrine Sedge Fen**	**Riverine Marsh**	**Lacustrine Marsh**
Carex spp.		126.9	474.6	294.8	97.5	877.7
Potentilla palustris		13.6	1.9	2.9		
Menyanthes trifoliata		19.5				
Grasses (Agrostis, Scabra)		1.6				
Triglochin maritima		1.4				
Smilacina trifolia	6.1					
Rubus chamaemorus	20.2					
Eriophorum vaginatum	3.6					
Typha latifolia						54.9
Equisetum fluviatile			3.7			
Calamagrostis spp.					189.2	
Urtica dioica					1.8	
Mentha arvensis					0.4	
Galium trifidum					1.0	
minor spp.		2.7	0.1	0.7	6.8	
Salix spp.	3.6	8.7		12.2		
Andromeda polifolia	19.8	38.7				
Oxycoccus quadripetalus	10.9	4.4				
Ledum groenlandicum	65.1					
Vaccinium vitis-idaea	21.7					
Betula pumila				1.7		
Picea mariana	27.0					
Total production	**178.0**	**217.4**	**480.3**	**312.3**	**296.7**	**932.6**